Unfamiliar face recognition: How we perceive and remember new faces

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Thesis submitted for the Degree of Doctor of Philosophy

May 2013

Declaration

I declare that this thesis was composed by myself, that the work contained herein is my own, and that this work has not been submitted for any other degree or professional qualification.

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15th May 2013

Publication note

Experiment 2 reported in Chapter 4 of this thesis has been published in the Journal Neuropsychologia. Experiments 3 and 5 described in Chapters 5 and 6, respectively, are currently in preparation for publication.

Abstract

Most humans are experts in recognizing faces of familiar individuals, but are poor at individuating unfamiliar faces. The discrepancy between these two types of face recognition suggests qualitative differences in the perceptual encoding and memory storage of familiar and unfamiliar faces, yet little is known about the neural basis of these differences. In the present thesis, behavioural and event-related brain potential (ERP) measures were combined to investigate the mechanisms that underlie the perception and recognition of unfamiliar faces. The first two experiments investigated whether memory traces for unfamiliar faces are based on low-level view-dependent or more high-level view-independent codes. Results provide strong evidence for a qualitative change from strictly view-dependent to view-independent representations in visual face memory as initially novel unfamiliar faces become more familiar. A second series of three experiments examined whether identity-specific cues are processed in an optional or an obligatory fashion. Findings suggest that the perception of facial identity is strongly task-dependent (i.e., optional), even for famous faces, but can also show a degree of mandatory processing when identity is task-irrelevant. The sixth study examined the persistence of perceptual memories of unfamiliar faces and revealed a substantial weakening of face representations in visual working memory over short periods of time. The final experiment investigated the neural basis of developmental prosopagnosia (DP). Results demonstrated spared identity-sensitive processing in DP participants, indicating that their face recognition deficits do not always result from severely disrupted visual face recognition processes. However, despite evidence for perceptual learning of invariant aspects of face structure, these processes seemed to be inefficient in individuals with DP.

Taken together, this thesis explored how we perceive and remember individual unfamiliar faces. Results indicate that unfamiliar face recognition is mediated by fast and flexible (i.e., strongly task-dependent) identity-specific visual processes, which rapidly become view-invariant during face learning.

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Acknowledgements

I am deeply grateful to Professor Martin Eimer and I would like to give my sincere thanks to his invaluable support and hands-on mentoring throughout the PhD process. Many thanks for introducing me to the academic world of research, and for sharing his expertise and enthusiasm for science with me.

I sincerely thank Dr Angela Gosling for her continuous help and advice, Dr Anna Grubert for her tireless support and encouragement, and John Towler for stimulating discussions. I am grateful to Sue Nicholas for her invaluable help in teaching me how to program and run EEG experiments, and to Dr Monika Kiss, Dr Silvia Dalvit-Ménabé, Dr Paul Matusz and Joanna Parketny for their help at various stages of my PhD studies.

My final big thank you goes to my parents for their love and support, and to my boyfriend, Arnaud, for always being there for me.

Chapter 1. Introduction to human face perception

Humans are surprisingly skilled in recognizing thousands of individual faces despite their structural similarity, and despite large variations in their visual appearance. However, our 'face expertise' does not seem to apply equally to the identification of unfamiliar faces (i.e., novel faces that have only been encountered a few times). Behavioural evidence from face memory studies has highlighted marked differences in our ability to identify familiar as compared to unfamiliar faces. Face recognition across dynamic changes in facial or low-level visual attributes (e.g., changes in expression or lighting) is excellent for familiar faces but surprisingly poor for unfamiliar faces (e.g., Hancock, Bruce, & Burton, 2000). These findings suggest that that there are differences in the way in which familiar and unfamiliar faces are processed and represented in visual face memory, yet there is little insight into the underlying neural basis of these differences. The present thesis is an investigation of the neural processes that underlie our perception and recognition of individual unfamiliar faces. Three lines of research were addressed. First, what type of information is acquired from an unfamiliar face? Are visual memory traces of unfamiliar faces based on view-dependent (*pictorial)* or view-independent (*structural)* codes? Second, what are the roles of attention and top-down task relevance in face identity processing? Are identity-specific facial cues processed in an optional (i.e., task-dependent) or an obligatory fashion? And finally, what is the neural basis of severe face recognition deficits in individuals with developmental prosopagnosia?

The present chapter begins with an introduction to why faces are "special" (Section 1.1), followed by an outline of cognitive and neuroanatomical models of face recognition (Sections 1.2 and 1.3, respectively). Current insights into the neural systems for the perception of familiar relative to unfamiliar faces will be presented (Section 1.4). Finally, acquired and developmental types of prosopagnosia (AP versus DP) will be described (Section 1.5), and the neural basis of DP will be discussed (Section 1.6).

1.1 Why faces are special

Human faces are fascinating. Infants preferentially attend to and interact with faces, and faces remain the most important objects in our visual world. Perceiving and remembering faces are essential cognitive abilities for social interactions and it is remarkable how the

human brain memorizes thousands of individual faces that we encounter during a lifetime. While there is no doubt that faces are important and in that sense "special", a long-standing debate in face research concerns whether or not faces are processed by dedicated visual mechanisms. In other words, are faces processed by distinct and possibly innate brain regions in human visual cortex, so-called 'face modules'? Two different accounts have been put forward to explain a large body of data indicating specialized neural processes for the perception of human faces.

On the one hand, it has been proposed that there exists a distinct module that is exclusive for face perception and may have evolved evolutionary due to the social importance of faces ('modular hypothesis'; e.g., Farah, 1996; Yovel & Kanwisher, 2004). On the other hand, the existence of a dedicated 'face module' has been challenged by the argument that special processing mechanisms are engaged for faces because they are visual stimuli with which humans have acquired a high level of perceptual expertise ('expertise hypothesis'; e.g., Diamond & Carey, 1986). The following section will outline evidence for both accounts.

1.1.1 The 'modular' hypothesis

One account of human face perception assumes that the visual cortex is subdivided into anatomically and functionally distinct 'modules', and that one of these is exclusively recruited for the processing of faces. The innate nature of such a face module implies that it is already present in infants, which is supported by findings that infants preferentially attend to human faces (Morton & Johnson, 1991), which may suggest that humans possess a structural face template from birth. Another line of research has provided further evidence for a special status of faces. Findings from Tanaka and Farah (1993) showed that faces are processed differently from objects, and that the perception of faces, unlike other visual objects, relies on the integration of information from across the face. While recognition memory for a specific facial feature (i.e., Jim's nose) was good in the context of the whole face, performance was impaired when the face part was presented alone, referred to as the 'part-whole effect'. In contrast, no such effect was found for other objects. This demonstrates that face processing relies disproportionately more on 'holistic processing', the perceptual gluing of face parts into a whole that cannot or only to a limited extent be decomposed. Throughout this thesis, the terms *holistic* and *configural* will be both used to refer to the perception of a human face "in

one piece" (but see Gauthier & Tarr, 2002, for a distinction of the terms *holistic* and *configural*).

Another perceptual phenomenon indicating qualitative differences in the processing of faces relative to other objects is the 'face inversion effect' (Yin, 1969), which refers to impaired recognition memory for upside-down (or inverted) faces. The inversion effect is disproportionately larger for faces than for other objects, and has been attributed to disrupted configural-holistic processing due to the difficulty to extract spatial configurations from faces that are turned upside-down (Farah, Tanaka, & Drain, 1995). Along similar lines, aligning the top half of a famous individual with the bottom half of another famous face results in the illusion that the two half faces are fused together to produce a novel face (i.e., the 'composite face effect'; Young, Hellawell, & Hay, 1987; Carey & Diamond, 1994). This finding has been replicated using famous as well as unfamiliar faces, and has also been reported when merging the inner features of one face with the external features of another face (Hole, 1994). The composite face effect demonstrates that faces are processed 'in one piece' whereby different facial features are merged instantly creating a new holistic representation. Despite converging evidence for global-holistic processing for faces, the perception of local facial features also plays a role in face recognition. Findings from Itier, Alain, Sedore, and McIntosh (2007) showed that when participants had to identify previously learned faces by particular features, isolated eyes resulted in the best recognition performance. Further evidence for a special focus on the eyes in face recognition has been reported in 4-year-old children (Taylor, Edmonds, McCarthy, & Allison, 2001), suggesting that the processing of the eyes develops prior to face processing, which is likely to reflect the social function of eyes to convey emotions.

Strong support for specialised visual processing of faces comes from brain lesion studies, demonstrating selective deficits in identifying and naming faces following damage to the inferior temporal lobe (Damasio, Damasio, & Van Hoesen, 1982). Others have also shown the existence of selective face recognition deficits in brain-damaged patients. For example, Farah (1996) reported an acquired prosopagnosic who was severely impaired in recognizing faces but performed normal on other object recognition tests. In addition, functional neuroimaging (fMRI) studies have identified a distinct brain region in human lateral fusiform gyrus, referred to as the 'fusiform face area' (FFA), which responds selectively to face stimuli over other object classes (Kanwisher, McDermott, & Chun, 1997; Gauthier et al., 2000b). These findings

have been taken as evidence that distinct brain regions are involved in the perceptual recognition of faces and that impaired face recognition is caused by selective damage to these face modules.

Overall, existing data suggest that face perception and recognition is based on representations of individual faces that integrate both configural-holistic and feature-based information (McKone & Yovel, 2009) whereby the merging of distinct features into a global face configuration occurs instantaneously.

1.1.2 The 'expertise' hypothesis

The research reviewed so far clearly favours the view that face-selective neural mechanisms underlie human face perception. However, another line of evidence challenges the view of such a purely innate face module. The 'expertise hypothesis' put forward by Diamond and Carey (1986) argues that special processing mechanisms in human visual cortex are not dedicated to faces but to stimuli of perceptual expertise. Humans are highly skilled in detecting subtle perceptual differences between individual faces, but less skilled in differentiating within-category exemplars of other object classes. It has therefore been argued that faces are not innately special but merely reflect a high level of perceptual expertise with a particular stimulus class (i.e., faces) that humans have acquired over a lifetime. In line with this view, face-selective brain regions including the FFA are not uniquely tuned to the processing of faces but can be recruited by any object category with which humans have acquired perceptual expertise. Consequently, apparently face-specific mechanisms may in fact be expertise-specific mechanisms (e.g., Tanaka & Gauthier, 1997; Gauthier, Skudlarski, Gore, & Anderson, 2000a). Consistent with these predictions, several studies have indeed reported enhanced neural processing in human 'face-selective' areas to non-face objects of visual expertise (e.g., Tarr & Gauthier, 2000). A similar finding has been obtained with artificial stimuli that display a complex face-like spatial configuration, so-called 'Greebles'. Gauthier, Tarr, Anderson, Skudlarski, and Gore (1999) showed that following (but not prior to) extensive perceptual training, face-selective brain regions showed an increased neural response to Greeble stimuli which has been attributed to increased visual expertise in identifying individual Greebles.

In summary, there does not seem to be a simple answer to the question of why faces are special. A large body of research indicates the existence of face-selective neural processes in

human ventral cortex. However, some of these highly tuned face areas can also be recruited by stimuli of expertise. Considering the high face expertise in humans, it is rather difficult to dissociate the unique contribution of perceptual expertise in relation to any innate face processing mechanisms. Therefore, human face perception may be best described in terms of an integrative framework, which recruits a core network of effective neural processes of which some, but not all, may be exclusive for faces. Face-specific modules may thus operate in concert with other more general perceptual processes, and these latter processes are modulated by perceptual expertise.

1.2 Cognitive models of face recognition

Several functional models have been put forward to describe the complex cognitive architecture underlying human face perception (e.g., Bruce & Young, 1986; Burton, Bruce, & Johnston, 1990). The difficulty of such a model is to incorporate the sequence of different face processing stages from the perception of a basic perceptual to a refined post-perceptual semantic face representation. In addition, such a model has to account for the visual analysis of different types of facial attributes that can be derived from faces.

1.2.1 The Bruce & Young model

In 1986, Vicky Bruce and Andy Young proposed the, until today, most influential functional model of face recognition derived from an extensive study of documented everyday failures in recognizing faces (Young, Hay, & Ellis, 1985). Based on the nature of these typical recognition difficulties, the classic Bruce and Young (1986) model was developed which proposes several defining features of the human face recognition system. Figure 1.1 shows Bruce and Young's model illustrating the proposed functional modules and the distinct sequence of face processing stages. First, the model assumes that different facial attributes are processed in a sequence of discrete processing stages. Evidence for the sequential nature of human face perception came from the finding that recognition deficits can affect different aspects of faces. One example for this is when a face looks highly familiar but the person's name cannot be retrieved. These findings imply that a series of functional stages underlies successful face recognition.

Secondly, the model distinguishes between different types of information that can be extracted from faces, which are called 'codes'. When encountering a face, the structural components of a face (i.e., facial features and their configuration) are processed first. In this

visual-perceptual 'structural encoding' stage, changeable image-specific information (*pictorial* codes) is derived, such as the view or facial expression in which a face is encountered. This is followed by the processing of abstract face properties *(structural* codes) that refer to the basic structural components of an individual face that distinguish it from any other face and are essential for face recognition. These latter codes are abstract and invariant to any dynamic facial aspects. This dual route for the processing of pictorial and structural codes implies that unique facial identity is represented in a distinct functional module in the human brain

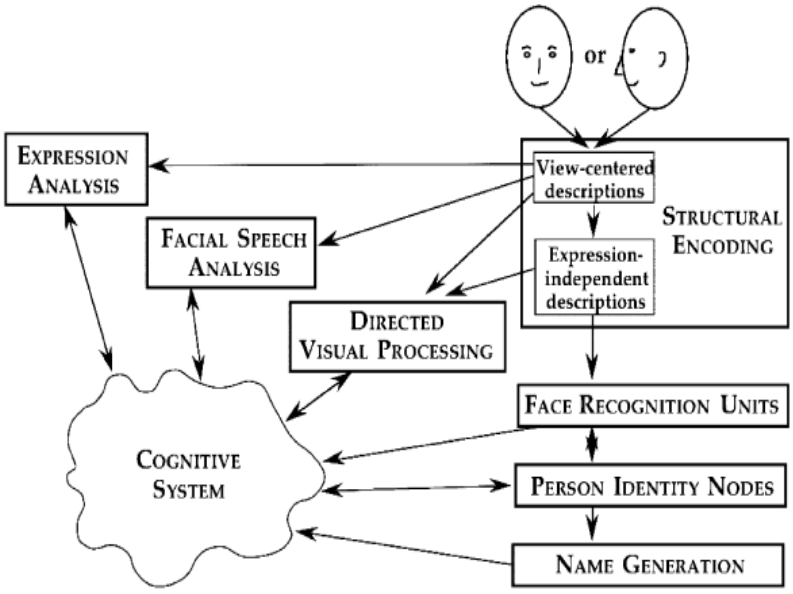


Figure 1.1 Bruce and Young's functional model of face recognition

Once invariant facial codes are extracted, these are then matched with stored visual face representations called 'face recognition units' (FRUs). A familiar face is successfully recognized when structural codes match with FRUs in long-term face memory. A successful match then further activates semantic information about an individual person (i.e., episodic 'person knowledge'), referred to as 'person identity notes' (PINs). PINs are regarded as convergence nodes and can be activated by cross-modal input (i.e., voices). This stage is followed by the name generation of a familiar face. An important assumption of the model is that different types of facial information are processed in relatively separate processing paths enabling either identity recognition (via FRUs and PINs), retrieval of semantic information from a face (i.e., gender), or recognition of facial expressions. Moreover, each of the face modules in the core system is further linked to other general cross-modal modules that are

involved in the analysis of facial expression, facial speech (i.e., lip reading) and directed visual processing (i.e., attention).

To date, the Bruce and Young model is the prevalent functional account of face recognition (for an adapted recent version see Schweinberger & Burton, 2003). Even though highly influential, the exact nature of how different functional modules are organized and interact with one another and to what extent they reflect independent processes is still a matter of debate and requires on-going research.

1.3 Neural substrates of face perception

Bruce and Young's (1986) functional face architecture provides an influential framework of the interplay between distinct functional modules in human ventral cortex. However, it does not specify where these modules are localized in the brain. Early single-cell recordings in non-human primates demonstrated the selective nature with which some neurons responded to specific visual properties. This selectively has also been found for complex visual objects including faces (Sanghera, Rolls, & Roper-Hall, 1979). Several studies have since confirmed the existence of face-selective cells in the temporal cortex of monkeys that respond most strongly to faces than to other types of objects (Desimone, 1991). Some of these 'face neurons' respond preferentially to individual facial features or combinations of features (Perrett, Rolls, & Caan, 1982) or to the identity or expression of a face (Hasselmo, Rolls, & Rolls, 1989). A large number of those 'face neurons' is grouped together to form distinct 'face clusters' in human visual cortex.

Several functional magnetic resonance imaging (fMRI) studies have investigated the organization of the neural system for face perception in human visual cortex (for ERP research see Chapter 2). These studies have identified distinct brain areas that respond more strongly to faces than other visual objects. In particular, a distinct region in the fusiform gyrus showed maximal neural activity to faces relative to other visual stimuli, referred to as the 'fusiform face area' (FFA; Kanwisher et al., 1997; Grill-Spector, Knouf, & Kanwisher, 2004). Given the face selectivity of the FFA, it has been argued that the FFA may represent a neural correlate for a 'face module', a specialized anatomical module for human face perception (Kanwisher, 2000). However, others (Haxby, Hoffman, & Gobbini, 2000; Ishai, Schmidt, & Boesiger, 2005) propose that a distributed neural network including multiple cortical regions mediates face

perception instead of a single cortical region. According to this view, multiple brain areas are differentially engaged in the processing of different types of facial attributes.

1.3.1 Haxby's model

Haxby and colleagues (2000) put forward a neuroanatomical model of face perception linking different functional sub-processes of face perception to distinct cortical regions. Figure 1.2 illustrates "core" and "extended" system of the model and their functional organization. The core system consists of visual extrastriate areas for the visual analysis of faces while the extended system comprises of additional neural systems that are involved in extracting various types of non-visual facial information (i.e., person semantics, voices or facial expressions). The core system is made up of three bilateral extrastriate regions, which include the inferior occipital gyrus – the occipital face area (OFA; Gauthier et al., 2000b), the lateral fusiform gyrus – the fusiform face area (FFA) and the posterior superior temporal sulcus (pSTS; Haxby et al., 2000; Hoffmann & Haxby, 2000). Additionally, neighbouring regions in ventral occipito-temporal cortices are also involved in face perception responding significantly but not maximally to human faces (e.g., Ishai et al., 2005). In line with Bruce and Young's functional framework of face recognition, Haxby's model proposes a sequential stream of processing where distinct brain regions are selectively involved in the extraction of early perceptual and subsequent semantic information from faces.

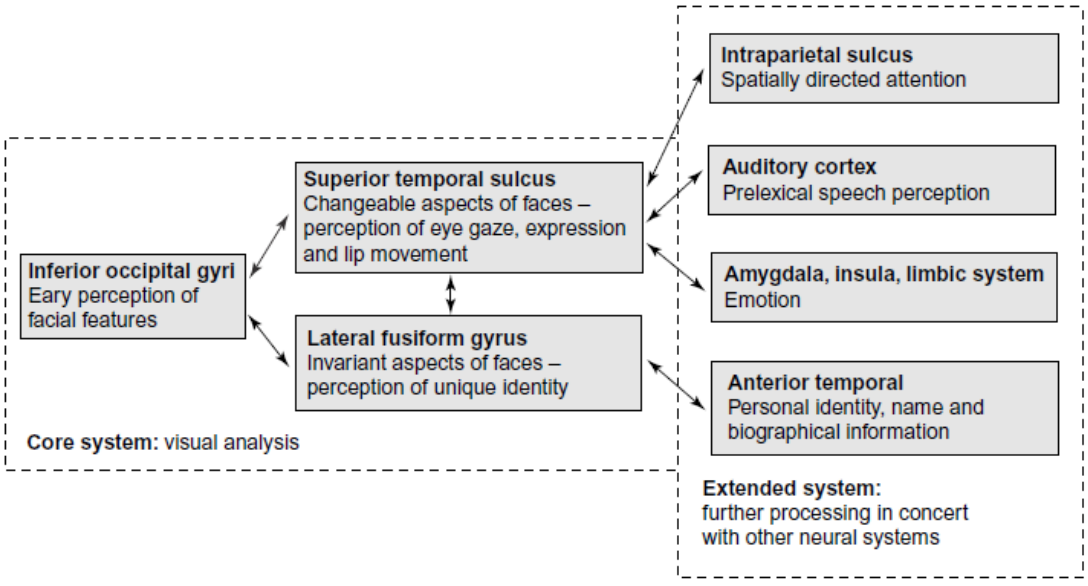


Figure 1.2 The distributed neural system for face perception (Haxby et al., 2000)

Figure 1.3 shows a flattened visual cortex in a single participant highlighting the three core face-selective regions in occipito-temporal cortex. Regions in red to yellow responded more strongly to faces than to houses (Haxby, Hoffman, & Gobbini, 2002), and were activated bilaterally but responses tended to be larger and more reliable in the right hemisphere.

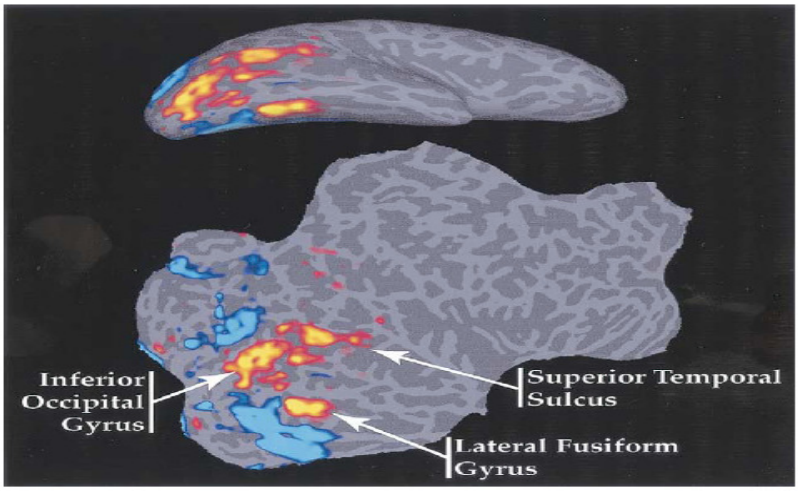


Figure 1.3 The three "core" extrastriate regions for face perception in human visual cortex (Haxby et al., 2002).

Initial stages of visual analysis of facial features involve neural activity in inferior occipital gyri (OFA; but see Rossion, 2008, for an alternative account of the role of the OFA in face perception) followed by two separate neural streams for the perception of individual identity and dynamic facial cues. The common anatomical route for the processing of changeable facial properties including facial expression and speech and has been linked to the posterior superior temporal sulcus (STS; Haxby et al., 2000). This is supported by findings from fMRI studies showing enhanced neural responses in the posterior STS but not the FFA for a variety of social facial cues including eye and mouth movements (Puce, Allison, Bentin, Gore, & McCarthy, 1998; Allison, Puce, & McCarthy, 2000), and changes in viewpoint (Andrews & Ewbank, 2004). In contrast, the perception of stable facial aspects that define individual identity has been linked to the lateral fusiform gryus (e.g., Grill-Spector et al., 2004; Gauthier et al., 2000b). However, the processing of changeable and invariant aspects of faces may be rather partial than completely distinct as reflected by enhanced neural responses to emotional facial expressions in both FFA and STS (Vuilleumier, Armony, Driver, & Dolan,

2001). Even though there appears to be some processing overlap, the selectivity of neural responses in the FFA (for identity recognition) and STS (for social cues from faces) indicates that these two anatomical regions are preferentially tuned to the processing of specific facial aspects. Therefore, the processing of unique identity proceeds relatively independently from the perception of dynamic facial cues, and is largely, but not exclusively, mediated by one specific brain region.

While initial stages of perceptual face processing are limited to the core system, later stages recruit additional brain regions that make up the extended system and act in concert with the core regions. The extended system comprises of several cortical regions that are engaged in emotion processing (amygdala), voice and speech recognition (auditory cortex), visual attention (parietal regions) and biographical memory (temporal regions). The overall strength of the neural response is thus mediated by additive responses in both core and extended system. For example, the encounter of a familiar face does not only activate the core system for identity perception but also elicits an emotional response to the familiar individual as well as the retrieval of person knowledge. This highlights the importance of the extended system in aiding the retrieval of different types of facial information during social interactions.

In summary, neuroimaging research has shown that multiple anatomically distinct 'face areas' can be identified in human visual cortex responding most strongly to faces than other visual objects. Haxby's neuroanatomical model of human face perception links distinct brain regions to the selective processing of different types of facial aspects where face processing is mediated by a core system for the early perception of facial features and an extended system where specific facial information receives further processing. In addition, a defining principle of the core system are two anatomically dissociable processing streams for the processing of invariant facial identity as compared to changeable social cues**.**

1.4 Neural systems for familiar versus unfamiliar face perception

Humans acquire familiarity with a face through countless encounters. While the Bruce and Young (1986) model provides a good framework of the basic architecture underlying familiar face recognition, it does not specify how the brain recognizes unfamiliar as compared to familiar faces. Does the perception of familiar and unfamiliar faces engage different neural processes? The term *unfamiliar* will be used throughout this thesis to refer to faces that are

initially novel but gradually become *visually familiar* following repeated exposure to the same faces. However, it has to be noted that representations for newly learned unfamiliar faces should still considerably differ from rich perceptual representations for familiar (or famous) faces, which have been acquired during many encounters on very different occasions.

Even though humans are often referred to as 'face experts', there are striking differences between our face recognition ability for familiar as compared to unfamiliar faces. Behavioural evidence suggests that most humans are excellent at recognizing familiar faces but surprisingly bad at recognizing unfamiliar faces, and this is the case across different paradigms and experimental tasks. For example, findings from face memory studies have consistently shown that familiar faces are identified faster and more accurate than unfamiliar faces (Ellis, Shepherd, & Davies, 1979) and even in low quality images recognition of familiar relative to unfamiliar faces remains good (Burton, Wilson, Cowan, & Bruce, 1999). In another study (Bruce et al., 1999) participants had to identity whether or not a target face was present among a line-up of faces, one of which could be an image of the target face taken with a different camera. Thus, target faces at learning and test differed in low-level visual properties, while structural information about unique facial features was unchanged. A high error rate of 30% for both target-present and target-absent arrays demonstrated impaired face recognition when different photographs of the same person were used between learning and test. Similarly, recognition advantages for familiar over unfamiliar faces have been found across a variety of image changes including variations in low-level information such as lighting (Hill & Bruce, 1996) and changes in facial attributes such as expression or view (Bruce, 1982). Further evidence for dissociable neural mechanisms for the perception of familiar versus unfamiliar faces comes from neuropsychological research. Some brain-damaged patients perform normal when matching the identity of unfamiliar faces, despite having lost the ability to recognize familiar faces (Bauer, 1984). The opposite effect has also been shown, where a patient is completely unable to recognize unfamiliar faces but performs normal on familiar face matching tests (Malone, Morris, Kay, & Levin, 1982). These findings suggest that different neural correlates underlie familiar and unfamiliar face processing.

In line with Bruce and Young's (1986) model, recognition of a familiar face relies on the perceptual analysis of *structural* codes containing those facial features that specify identity and these codes are obtained during repeated encounters with an individual face. In contrast, the perception of unfamiliar faces is based on low-level *pictorial* codes that are specific to the

encountered image. Therefore, the main difference between unfamiliar and familiar face recognition lies in the ability to perceive and store invariant facial cues for facial identity that are essential for recognition. Moreover, viewing a familiar face activates not only rich long-term memory representations but also semantic information about that individual (i.e., person knowledge). In contrast, unfamiliar faces are represented as transient visual face memories based on very few encounters. In other words, while familiar faces activate a variety of facial codes among which visually-derived structural and semantic codes, unfamiliar faces are represented as pictorial snapshot-like images.

It has been proposed that, as novel faces become more familiar, low-level pictorial codes are gradually converted into more high-level abstract visual representations, thereby reducing the need of face recognition processes to rely on pictorial information (Burton, Jenkins, Hancock, & White, 2005). Therefore, the transition from unfamiliar to familiar faces could be thought of as a process where successive encounters with a face refine and adjust an 'average' face template of that particular individual thereby gradually changing an image-based into a flexible and more robust perceptual face representation (Burton et al., 2005). According to this view, increasing exposure to a particular face helps to eliminate much of the individual low-level variability that is found across different images of the same individual. In this sense, face learning may reflect the refinement of an individual face template allowing the effortless distinction between identity-related and image-based information**.**

Taken together, converging evidence from behavioural and neuropsychological studies suggests that familiar faces are processed qualitatively differently from unfamiliar faces. Familiar face recognition is thought to rely on the activation of high-level abstract representations that contain structural information about a face which are invariant across different images of the same person. In contrast, newly acquired perceptual memories of unfamiliar faces are based on low-level information about the encountered image, and are therefore affected by image-related visual changes. This suggests that repeated exposure to an individual face fundamentally alters the underlying perceptual processes, and that robust structural representations of familiar faces emerge as a result of face learning.

1.4.1 Neural markers of face familiarity

Given the clear behavioural recognition advantage for familiar relative to unfamiliar faces, surprisingly little evidence points to qualitative differences in the underlying neural response

(see Natu & O'Toole, 2011, for a review). This contrasts markedly with the reliable finding that familiar face recognition is easy while unfamiliar face recognition is poor (Burton & Jenkins, 2011). While much research has focused on identifying brain regions that are involved in the processing of familiar faces, relatively few studies have investigated the neural basis of familiar as compared to unfamiliar face perception. In macaques, face-selective cells showed enhanced neural responses to familiar as compared to unfamiliar faces while the relative strength of this response increased as a function of increasing familiarity (Wallis & Rolls, 1997).

Findings from human neuroimaging studies have yielded inconsistent results as to whether familiar and unfamiliar face processes can be dissociated in fusiform face areas. Leveroni et al. (2000) reported larger neural responses to famous as compared to newly learned or novel unfamiliar faces over prefrontal and lateral temporal regions, which are thought to reflect the activation of 'person knowledge' and episodic memories of a familiar person. However, neural responses in the fusiform gyrus (FG) did not distinguish between familiar and unfamiliar faces. Some evidence has begun to emerge which suggests that neural activity in the fusiform gyrus is modulated by the familiarity with a face. In a multistudy analysis of positron emission tomography (PET) studies, Rossion, Schiltz, and Crommelinck (2003) showed that face-selective responses in right FFA and OFA were significantly larger to familiar as compared to unfamiliar faces. Ewbank and Andrews (2008) tested whether the relative view-dependence of the fusiform face area (FFA) is modulated by face familiarity. A reduction in FFA activity was observed to repetitions of the same familiar face shown from different viewpoints, but not to repetitions of two different views of an unfamiliar face. These results might provide a neural basis for behavioural differences in the recognition of familiar and unfamiliar faces. Similarly, Eger, Schweinberger, Dolan, and Henson (2005) showed that familiarity with a face enhances the view-independence of face representations in face-selective brain regions. For familiar faces, face-selective areas in anterior fusiform cortex generalised across different images of the same person, while the same regions failed to adapt when the same unfamiliar face was repeated in a different view. Further support for stronger neural activation in the core system for face perception for 'previously seen' faces relative to novel faces comes from Ishai and Yago (2006). Additionally, larger neural responses to previously seen faces were found in parietal and prefrontal regions, and the hippocampus, which are thought to reflect the retrieval of a memory trace of the first

encounter with a face. A study by Leube, Erb, Grodd, Bartels, and Kircher (2003) further suggests that the recognition of newly learned faces activates a dorsal pathway in the temporal lobe, which might be responsible for a "feeling of familiarity". In contrast, the ventral pathway may be mainly involved in face identity processing.

Overall, the reviewed research suggests that differences in the perception of familiar versus unfamiliar faces reflect largely quantitative rather than qualitative changes in core face-selective regions. However, some fMRI evidence suggests that neural activity in the FFA to familiar but not unfamiliar faces is invariant to image transformations such as view changes, which indicates different underlying perceptual mechanisms for these two types of face recognition. Moreover, inconsistent findings in the neuroimaging literature may be partly attributable to different degrees of familiarity with faces, or may reflect differences in task-related and/or attentional processing. More research into the mechanisms of unfamiliar and familiar face recognition is needed to clarify their neural basis.

1.5 Prosopagnosia

While the reviewed studies so far have provided important insights into the typical face recognition architecture, studying cases where face recognition fails can provide important additional insights. Research on disorders in face perception have added a great deal to our present understanding of the intact face recognition system and provide strong evidence for the existence of a specialized face module in the human brain. A distinction has been made between face recognition impairments that are acquired due to brain injury (i.e., neuropsychological) or present since an early age in the absence of any anatomical damage (i.e., neurodevelopmental). The focus of the present thesis is on prosopagnosia, a selective perceptual deficit in recognizing individual faces, which can emerge during early development or as a result of brain injury.

It is generally believed that humans are experts in remembering thousands of individual faces. However, recognizing a person by its face is an extremely difficult task for individuals with prosopagnosia (also called facial agnosia or face-blindness), as all faces seem to look the same. The term prosopagnosia was first coined by Bodamer (1947) and derives from the ancient Greek words 'prosopon' meaning face and 'agnosia' meaning non-knowledge. Prosopagnosia does not result from general deficits in visual or visual memory processes as faces can be distinguished from other objects (i.e., no general agnosia), and a person can be

identified by other means such as their voice (i.e., no amnesia for individuals). However, the condition disproportionately affects face recognition relative to the recognition of other objects, even though some impairment for within-category object recognition is often present. Different types of prosospagnosia can be distinguished based on the specific type of impairment and the nature of the condition. The two main loci of recognition deficits involve either the early visual analysis of facial features or subsequent post-perceptual processing stages where semantic information is activated. The former type is referred to as 'apperceptive' and the latter as 'associative' prosopagnosia (De Renzi, Faglioni, Grossi, & Nichelli, 1991). A second distinction relates to the onset of this condition. While the first reported cases of prosopagnosia were linked to acquired brain lesions, only recently have cases been reported without any apparent neurological origin suggesting a very early developmental onset. Research into both acquired and developmental prosopagnosia will be outlined in the following section.

1.5.1 Acquired prosopagnosia (AP)

In acquired cases, an intact face recognition system is damaged due to an injury (e.g., tumour or stroke) to those cortical regions that mediate individual face recognition. The first cases of acquired prosopagnosia (AP) emerged in the late 20th century. Bodamer (1947) documented patients with brain damage to occipito-temporal cortical regions, which had lost the ability to identify individual faces. The finding that damage to distinct cortical areas causes a recognition impairment that is selective for faces supports the existence of a functionally and anatomically dissociable brain area for face perception. However, given the often diffuse nature of the lesions sites, identifying the exact brain regions affected in AP is a difficult task. Some individuals with AP show unilateral right hemisphere occipito-temporal lesions (De Renzi, Perani, Carlesimo, Silveri, & Fazio, 1994) while bilateral lesions have also been found (Damasio et al., 1982), demonstrating the importance of effective interactions between both hemispheres for face recognition. Findings from fMRI studies present a heterogeneous picture of neural responses to faces in acquired prosopagnosics. For example, Schiltz et al. (2006) reported abnormal fMRI adaptation in a patient with damage to the right inferior occipital gyri (rIOG), where neural responses in right middle fusiform gyri (rMFG) did not discriminate between repeated presentations of the same face, relative to two different faces. Others (e.g., Sorger, Goebel, Schiltz, & Rossion, 2007) found typical enhanced neural

activity in fusiform regions to faces including right FFA, right STS and left OFA in an acquired prosopagnosic with a lesion to the right OFA, which further indicates that spared functional normality is not sufficient for effective face recognition. These findings indicate that successful face recognition depends on the integrity of multiple brain regions and that occipito-temporal face-selective regions besides the fusiform face area are necessary for face processing (see Rossion et al., 2003).

Another difficulty in assessing the functional neuroanatomy in individuals with AP relates to cortical plasticity where adjacent brain regions take over lost functions of damaged areas. However, the apparent face recognition deficits in AP indicate the limits of cortical plasticity, and the failure of intact brain areas to successfully compensate for damaged neural face processes highlights the selectivity of these regions for face processing. Considering the varied nature of behavioural face recognition deficits, the emerging picture indicates that AP is a heterogeneous condition where processing deficits selectively affect the perception of different types of facial information. As this condition results from damage to parts of an otherwise fully functioning face recognition system, individuals who acquire this condition show large differences in spared face recognition abilities reflecting the specific nature and location of the lesion size.

1.5.2 Developmental prosopagnosia (DP)

Only recently have cases of prosopagnosia been described that are characterized by a marked absence of known neurological damage (see Duchaine, 2011, for a review). The term developmental prosopagnosia (DP) has been used to describe this type of prosopagnosia, which is also referred to as congenital (i.e., present from birth) to emphasize the early onset of atypical face recognition processes. Similar to AP, DP is defined by a severe deficit in distinguishing individual faces, while other aspects of face processing are also often impaired, such as emotion recognition (e.g., Duchaine, Yovel, Butterworth, & Nakayama, 2006). The diverse nature of face processing deficits observed in DPs reflects the complex neural architecture of human face processing, where neural processes can break down at various stages during brain development. As for developmental prosopagnosics, an important question concerns whether these individuals posses an atypical face recognition system which is fundamentally different from the one in fully functioning adults or whether the overall face architecture is typical while damage is confined to sub-processes within the

system. The similarity of face-selective impairments seen in both AP and DP suggests that both conditions involve deficits to similar and therefore typically developed face processes.

Even though the neural basis of DP is still largely unknown, research indicates an important role of genetic factors in mediating face recognition abilities (Duchaine, Germine, & Nakayama, 2007; Wilmer et al., 2010). Most individuals with DP report difficulties recognizing faces from an early age, and some have affected family members, which suggests that this condition is likely to be hereditary and runs in families (Lee, Duchaine, Wilson, & Nakayama, 2010). Based on these findings, face recognition ability may be best described in terms of a continuum ranging from the high end of so-called "super-recognizers" to the low end of severe prosopagnosia (Russel, Duchaine, & Nakayama, 2009). Findings from relatively few fMRI studies have presented an inconsistent picture of neuroanatomical differences in DPs. Hadjikhani and de Gelder (2002) found that in two individuals with DP core face-selective regions including the FFA and OFA failed to discriminate between faces and other visual objects. Behrmann, Avidan, Gao, and Black (2007) reported anatomical differences in the size of the anterior fusiform gyri, which were significantly smaller in the DP group than a control group. Moreover, the relative size of this region correlated with behavioural face recognition ability. Others (e.g., Hasson, Avidan, Deouell, Bentin, & Malach, 2003) did not find qualitative differences in face-selective neural processes in right fusiform and occipital face areas between DPs and controls, but a small reduction in the neural response to faces in left occipital face areas in DPs. These few fMRI data suggest that DP does not result from qualitatively different neural mechanisms for face perception, but instead may reflect disruptions in the effective interplay of different face-selective regions.

In conclusion, DP is characterized by the absence of any known anatomical damage suggesting an early onset during brain development. The emerging picture of DP suggests a prominent role of genetic factors for face recognition ability where DP lies at one extreme end of a continuum. Furthermore, neuroimaging data do not highlight fundamental qualitative differences in face perception between DPs and typical adults but rather suggest that face-selective impairments arise due to either localized damage to specific face processes, or due to impaired integrity of the distributed face processing network. Dysfunctional mechanisms at different face processing stages could thus explain the varied nature of face recognition deficits in DP. Alternatively, an atypical face processing system might already have evolved during early brain development.

1.6 Neural basis of DP

1.6.1 Early perceptual deficits

A growing body of behavioural and neurophysiological evidence suggests that face-specific deficits in DP can emerge for two reasons. On the one hand, the early perception of faces and their configuration may function insufficiently to accomplish face recognition. On the other hand, critical connections between early perceptual and late semantic face processing stages may be broken. The first stage at which face processing can break down is during the initial perceptual analysis of facial features. Faces are typically processed in a configural-holistic manner that is crucial for the extraction of more abstract face representations that allow recognition across novel images (Young, et al., 1987). If configural face mechanisms fail in DPs, this should result in an overreliance on feature-based processing. This assumption is supported by the finding that DPs showed lower performance relative to controls when matching unfamiliar faces that were altered by either replacing eyes and mouth (*part task*) or by varying the relative position of eyes and mouth (*spacing task*; Yovel & Duchaine, 2006). This suggests that DPs employ a feature-matching strategy when recognizing individual faces, presumably due to inefficient holistic face mechanisms that merge individual facial features into a face configuration.

Several studies support the notion that impaired holistic processing underlies severe face recognition deficits in acquired and developmental types of prosopagnosia (see Ramon, Busigny, & Rossion, 2010, for abnormal holistic processing in an acquired case). Avidan, Tanzer, and Behrmann (2011) provided evidence for disrupted holistic processing in developmental prosopagnosia. A sample of 14 prosopagnosics with early developmental onset did not show the typical face inversion effect (better performance for upright compared to inverted faces) and also did not show interference from the task-irrelevant bottom half of composite face stimuli as seen in controls. A similar finding of impaired holistic face processing in DP has also been observed for different types of composite face tasks where top and bottom halves either showed two different identities, or two different facial expressions (Palermo et al., 2011). Further support for an early perceptual deficit in DP comes from the absence of a typical N170 face inversion effect (i.e., an enhanced neural response to inverted versus upright faces) in DP participants (Towler, Gosling, Duchaine, & Eimer, 2012). Taken together, these findings suggest that disruptions in holistic processing may underlie, at

least, some of the face recognition deficits in individuals with DP. Therefore, even though visual aspects of face processing can be spared, many DPs show some deficits in the perception of an individual's face as 'a whole'.

The ability to form holistic representations of faces is also assessed in standard neuropsychological tests of face recognition ability (see Duchaine & Nakayama, 2006, for the Cambridge Face Memory Test, CFMT), which requires the recognition of unfamiliar faces across different photographs, such as view changes and images with added noise. Performance on this test requires learning invariant structural (i.e., holistic) visual cues about the identity of unfamiliar faces, and low scores on this test reflect impairments in holistic face processing. However, not all DPs appear to rely on feature-based face recognition, but some show intact configural face mechanisms (Duchaine, 2000; see also Garrido, Duchaine, & Nakayama, 2008, for normal inversion effects in DP), confirming the heterogeneous picture of behavioural deficits in DP. This further suggests that there are several processing stages at which the human face recognition system can break down and that face processing impairments in some DPs occur at late post-perceptual stages where semantic person knowledge is activated.

1.6.2 The 'disconnection' hypothesis

So far, the reviewed research suggests that DP arises from dysfunctional face perception during early 'structural encoding'. However, evidence has started to emerge which suggests that face-selective impairments can also be caused during later post-perceptual processing stages where semantic information about faces is derived. These impairments could either reflect an inability to access semantic face memories (i.e., person knowledge) or broken links between visual and semantic face memory. Burton, Young, Bruce, Johnston, and Ellis (1991) propose that the dissociation between overt and covert face recognition results from disruptions between early perceptual and post-perceptual face processes, and therefore represent a 'disconnection phenomenon'. Interpreted in Bruce and Young's (1986) model, disrupted links between visual face representations (FRUs) and semantic face memories (PINs) may underlie severe face recognition impairments. A similar disconnection account has been put forward by Breen, Caine and Coltheart (2000) to explain dissociations between covert autonomic responses and impaired overt face recognition in prosopagnosia, which

may result from a breakdown in the ventral visual stream between two separable pathways for the perception of person knowledge, or facial emotion.

Electrophysiological evidence for broken links between early and late face-selective neural processes in DP comes from recent findings by Eimer, Gosling and Duchaine (2012). In this study, early perceptual N250 ERP responses systematically distinguished between familiar and unfamiliar faces, despite a complete lack of conscious recognition of those faces in DP participants. However, later semantic responses to familiar faces were absent demonstrating a disruption between intact visual and broken semantic representations of familiar faces, which highlights the importance of post-perceptual face processing stages for conscious face recognition. Therefore, face recognition deficits in some DPs appear not always to result from deficits in the visual aspects of faces but can arise from a failure to activate semantic person knowledge, reflecting a disconnection between perceptual and semantic face memory.

In summary, DP is a diverse condition defined by an inability to recognize individual faces, even though other aspects of face processing can also be impaired. The disproportionate perceptual deficit in processing individual faces as compared to other objects supports the view of underlying damage to face-specific neural mechanisms. Even though the neural basis of DP is still largely unknown, research suggests that selective deficits can arise at either early perceptual or late post-perceptual face processing stages. Overall, findings support the view that DP can be explained in terms of a neuropsychological framework, where localized face processing deficits occur within a typical face recognition system. These impairments can reflect early perceptual deficits in global-holistic face perception or disconnections between visual and semantic face memory.

Chapter 2. Method

An immensely useful method to identify the time course of face-specific neural processes is the analysis of event-related brain potentials (ERPs). ERP measures are characterized by an excellent temporal resolution, allowing researchers to track the temporal sequence of distinct processing stages in the human brain within a time range of milliseconds. Chapter 2 provides an introduction to ERPs (Section 2.1) followed by a literature review on two face-selective ERP components: the N170, which indexes structural encoding, and the N250/N250r, which has been linked to individual face recognition (Section 2.2). Finally, the use and underlying rationale of repetition paradigms in face research will be discussed (Section 2.3). The chapter finishes with an overview of the conducted research (Section 2.4).

2.1 Event-related brain potentials (ERPs)

Electroencephalography (EEG) is the recording of electrical activity from the scalp. The term EEG was first introduced by Hans Berger in 1929 who measured EEGs or “brain waves” from a single electrode on the human scalp. By amplifying the neural signal, he was able to obtain a graphic representation of voltage changes in neural activity between two different cerebral locations, plotted over time. EEG measures of voltage fluctuations resulting from ionic current flows within the neurons of the brain have been widely used in the last decades as markers of various brain states such as arousal or activity levels. In clinical contexts, EEG recordings of the brain's spontaneous electrical activity are used to detect abnormal neural activity in brain diseases such as epilepsy. EEG is a non-invasive technique and has the unique advantage of providing precise information about the time course of cognitive processes due to its excellent millisecond-range temporal resolution (Luck, 2005).

In the last decades, EEG measures have been extensively employed in neuro-scientific research as a powerful tool for investigating the temporal sequence of cognitive processes. While specific neural processes cannot be detected in raw EEG data, neural activity tied to a particular temporal event, such as the onset of a visual stimulus, can be extracted from the overall EEG by a simple averaging process. By averaging the EEG activity time-locked to the presentation of a particular stimulus, stimulus-related activity will add to the average of the event-related brain potential (ERP) waveform while neural activity that is unrelated to the stimulus will become gradually attenuated. ERPs thus index evoked time-locked neural responses that arise during sensory, cognitive or motor processing.

2.1.1 Neural sources of ERPs

The brain's electrical activity is maintained by billions of electrically charged (or "polarized") neurons caused by underlying chemical reactions in neurotransmitter activity that mediate the flow of information through the human brain. In the nervous system, much of the electricity activity is due to movement of small ions across cell membranes. Each neuron receiving synaptic inputs can be thought of as a small electrical dipole (i.e., consisting of two oppositely charged “poles”). The influx of positively charged ions during neurotransmission creates a negative voltage at other parts of the neuron. A dipole corresponding to a single neuron is not detectable with EEG, but when thousands of neurons receive synchronous synaptic inputs, dipoles sum together to yield strong voltage signals at the scalp. The voltage changes obtained at a single surface electrode side therefore reflect the summated electrical activity of postsynaptic potentials from dendrites and cell bodies of thousands of neurons. For the electrical signal to be measureable at the scalp surface, individual dipoles must have a similar spatial orientation, because if individual dipoles are not spatially aligned, oppositely oriented dipoles will cancel each other out. The most likely cell candidate eliciting the EEG signal is a wide network of cortical pyramidal cells, which are typically aligned in a perpendicular way. Furthermore, ERP responses are thought to reflect post-synaptic potentials that are created when neurotransmitters bind with receptors on postsynaptic neurons. In particular, ERPs are most sensitive to a particular set of post-synaptic potentials: Those generated in superficial layers of the cortex on the crests of gyri directly abutting and radial to the skull. In contrast, dendrites which are deeper in the cortex inside sulci or in midline or deep structures (such as the hippocampus) or produce currents that are tangential to the skull have far less contribution to the EEG signal. Moreover, unlike action potentials, postsynaptic potentials can be measured at a great distance, owing to their relatively long duration of tens or hundreds of milliseconds. Therefore, ERPs are thought to reflect massive synchronized increases in postsynaptic neural activity of multiple sources overlapping in time (Luck, 2005).

One limitation of EEG is its poor spatial resolution making it difficult to identify the exact loci of its underlying neural generators. This is due to the fact that ERPs reflect the sum of neural activity of different sources, and in principle an infinite number of neural sources could explain any unique ERP data pattern (referred to as the ‘inverse problem’). Moreover, the folded nature of the human cortex means that activity from deep cortical sources is more

difficult to detect than currents near the skull. In addition, the meninges, cerebrospinal fluid and skull "blur" the EEG signal, obscuring its intracranial source. However, because ERP measures provide excellent temporal resolution, they are superior to other neuro-scientific measures in investigating the exact time course of cognitive processes.

2.1.2 ERPs in psychological research

Since the first documented EEG recordings, numerous ERP studies have been employed using a large array of electrodes and complex data analyses techniques to investigate temporal dynamics of information processing in the human brain. Distinct sequences of ERP peaks that follow the onset of a stimulus have been linked to different neuro-cognitive processes. Typically, ERP average waveforms show a sequence of positive and negative voltage deflections that are called peaks, waves or components. The letters 'P' or 'N' are used to indicate positive-going or negative-going peaks with the number reflecting the latency or ordinal position (e.g., N1 refers to the first negative peak to a visual stimulus). The sequence of these peaks is thought to reflect the flow of information through the brain, and the latency of each wave is associated with the temporal onset of a given process. Topographic maps illustrate differences in neural activity across the scalp and index the loci of neural responses to a particular stimulus. Two types of ERP components have been distinguished: Exogenous components that are elicited by external stimulus-related factors (i.e., the physical properties of a stimulus) and endogenous components that are modulated by internal factors such as top-down attention (Luck, 2005).

ERP measures are not only highly suitable to answer questions about the nature and time course of specific neural processes but are also highly useful in two other ways. First, they provide a continuous measure of neural processes between stimulus onset and behavioural response, making it possible to determine which processing stages are affected by a particular manipulation. Therefore, ERPs provide information about stages of processing rather than just the final end result. Second, ERPs are independent of behavioural responses and therefore represent a tool to detect covert processing, allowing the study of brain activity in the absence of attention and/or conscious awareness. Taken together, EEG measures represent an excellent tool for neuroscience research in providing insights into the temporal dynamics and nature of neuro-cognitive processes in the human brain.

2.2 Electrophysiological correlates of face perception

Much ERP research has investigated the neural mechanisms that underlie our ability to perceive and recognize faces. Face recognition is thought of as a complex process where various kinds of facial information are extracted very rapidly and efficiently within the time range of a few hundred milliseconds. Different face-selective ERP responses have been linked to distinct face processing stages (i.e., perceptual or semantic). The main focus of the present thesis will be on ERPs components that are elicited during early perceptual face processing stages that include the perception of structural face configurations and individual identity.

2.2.1 Structural encoding/ N170

Electrophysiological studies have identified a negative-going neural response to faces at lateral posterior electrodes in the 140 - 200 ms post-stimulus time window, which is thought to reflect the earliest stage of the perceptual processing of a face. This component reaches its maximum ~ 170 ms (N170) and is the most prominent and widely studied visual ERP component (see Eimer, 2011, for a review). The N170 component has been consistently linked to the perceptual categorization of a visual stimulus as a face and its structural encoding. The N170 corresponds to the earliest visually evoked N1 component, reflecting a negative deflection at posterior regions to all visual stimuli.

The presence of an N170 component to faces has been first demonstrated in early studies of human face perception (Bentin, Allison, Puce, Perez, & McCarthy, 1996). Since then, many ERP studies have shown that human faces elicit larger amplitudes at occipito-temporal electrodes than other visual objects (e.g., Allison, Puce, Spencer, & McCarthy, 1999; Eimer, 2000d). The finding of reliable amplitude differences between the visual processing of faces relative to non-face stimuli suggests that the N170 reflects face-selective visual processes. The posterior N170 is usually accompanied by an enhanced positivity to faces at fronto-central electrodes, the vertex positive potential (VPP; Jeffreys & Tukmachi, 1992). N170 and VPP are likely to reflect the activity of the same face-selective neural processes located in posterior fusiform gyrus (Joyce & Rossion, 2005). Figure 2.1 (top panel) illustrates grand-averaged ERP waveforms to faces relative to houses at posterior electrodes P7/8 and midline electrode Cz (Eimer, 2011). Enhanced negativities are elicited to faces relative to houses at lateral occipito-temporal electrodes P7/8 (N170 components) and this effect is larger over the right hemisphere. These are accompanied by an enhanced positivity to faces relative to

houses (VPP), peaking at about 180 ms post-stimulus. Typical N170 scalp topographies are shown in Figure 2.1 (bottom panel) obtained by subtracting ERPs to houses from ERPs to faces. The N170 (marked in blue) is maximal over lateral occipito-temporal areas, whereas the VPP (marked in red) is maximal at the vertex.

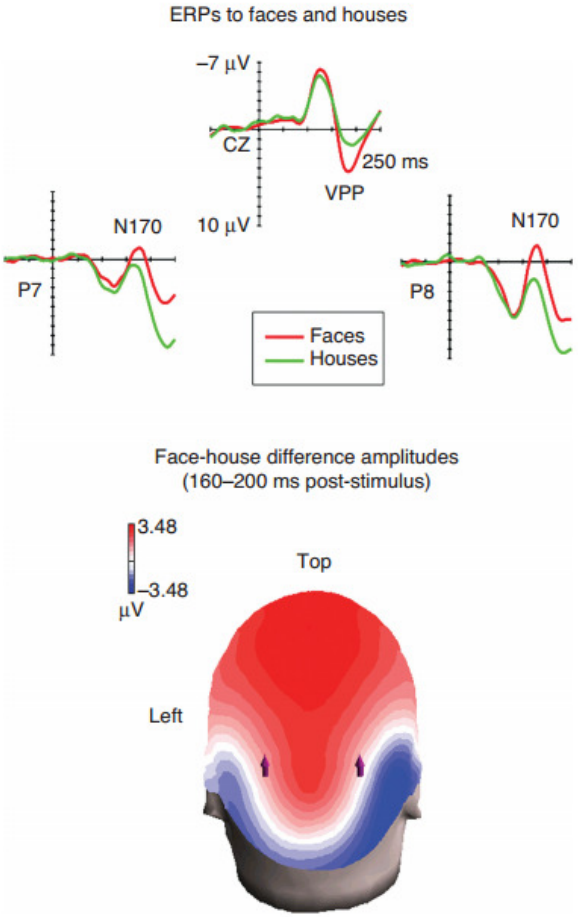


Figure 2.1 Top panel: Grand averaged N170 ERP waveforms in response to faces and houses. Negative amplitudes are plotted upward. Bottom panel: Scalp topography of ERP difference amplitudes in the N170 time window (160-200 ms after stimulus onset) obtained by subtracting ERPs to houses from ERPs to faces. Enhanced negativity for faces versus houses is shown in blue, enhanced positivity for faces versus houses in red (Eimer, 2011).

Existing data strongly suggest that N170 components reflect neural processes involved in the category-selective processing of faces, and in particular in holistic-configural face processing (Eimer, 2000d; Sagiv & Bentin, 2001). Most ERP studies have shown that the N170 reflects basic-level categorization prior to individual face recognition because of its invariance

to familiarity of faces (Bentin & Deouell, 2000) or face repetition (Eimer, 2000c; Schweinberger, Pfütze, & Sommer, 1995; but see Caharel, d'Arripe, Ramon, Jacques, & Rossion, 2009, for N170 adaptation effects to same face repetitions). This suggests that N170 components index the initial 'structural encoding' stage where global-configural face representations are obtained. Moreover, research suggests that the N170 reflects high-level face-selective visual processes. For example, George, Jemel, Fioric, Chaby, and Renault (2005) showed that two-tone 'Mooney' images elicited an N170 response only when those were presented upright and were identified as faces but not when they were presented upside-down and not perceived as faces. As Mooney faces share the same low-level visual properties in both the upright and upside-down condition, this finding reinforces the view that the N170 indexes the time at which a stimulus is perceived as a face. The generalizability of N170 components across different face formats including naturalistic faces, schematic faces (e.g., Sagiv & Bentin, 2001) or two-tone Mooney faces further indicate that a generic face template underlies the basic-level categorization of a face.

Strong support for the N170 as a neural marker of holistic-configural processing comes from studies demonstrating the sensitivity of this component to disruptions of face configurations. Face modifications at both the level of local features (by removing the eyes) as well as the global face configuration (by adjusting the distance between the eyes) have been shown to modulate N170 amplitudes. For instance, larger N170 components were found with increasing visibility of a face to which visual noise had been added (Jemel et al., 2003), demonstrating that the amount of visible configural facial information mediates the N170 response. One striking characteristic of the N170 is its strong modulation by face inversion (e.g., Eimer, 2000b; Rossion et al., 2000). Compared with upright faces, upside-down (or 'inverted') faces elicit N170 amplitudes that are delayed by about 10 ms and enhanced in amplitude. Face inversion is assumed to disrupt configural face processing, yet the underlying neural basis of N170 modulations to inverted faces is not fully understood. Along similar lines, increased N170 amplitudes and delayed onset latencies have been demonstrated to faces with removed internal or external features (Eimer, 2000d) as well as in response to isolated eyes (e.g., Bentin et al., 1996; Itier et al., 2007) or scrambled faces (George, Evans, Fiori, Davidoff, & Renault, 1996). Taken together, existing research suggests that N170 components are elicited by a variety of face or face-like images, and are still present even though enhanced in size to partial, incomplete or scrambled face-like configurations.

An ongoing debate in face perception research concerns whether the N170 reflects the neural activity of a domain-specific face mechanism (e.g., Carmel & Bentin, 2002). Several ERP studies have demonstrated that N170 amplitudes are modulated by visual expertise. For example, Tanaka and Curran (2001) compared N170 components elicited by stimuli of expertise to those obtained to novel stimuli. Larger N170 responses were elicited to stimuli within the area of participant's expertise (i.e., birds or dogs in bird or dog experts) relative to stimuli outside their area of expertise (i.e., dogs in bird experts or birds in dog experts). This finding indicates that early visual processing of objects from well-learned categories is different from that for less familiar objects. Others (e.g., Rossion, Gauthier, Goffaux, Tarr, & Crommelinck, 2002) reported similar effects of perceptual training on N170 latencies and amplitudes. In this study, participants were trained to distinguish face-like 'Greeble' stimuli whose complex spatial configurations are similar to those of faces. Following intensive perceptual training, a similar N170 response was observed for both faces and Greebles. Furthermore, following training delayed N170 amplitudes emerged to inverted Greebles in the left hemisphere, whereas the typical inversion-induced delay to faces is right lateralized. These findings demonstrate that the N170 component is modulated by visual expertise, but the exact nature of these modulations is as yet unknown. It is possible that N170 components are largely, but not exclusively, driven by innate face-specific processes, and that these responses reflect the activation of multiple cortical regions of which some are also recruited by complex non-face stimuli of visual expertise.

In summary, the current findings suggest that the N170 indexes early perceptual face processing stages where a visual stimulus is perceived as a face and its generic structural components are encoded prior to individual face recognition. In particular, N170 responses have been shown to reflect configural-holistic face processes that underlie the perception of a face stimulus as 'a whole' based on a generic face template. Moreover, the finding that N170 components generalize across different face formats indicates that it does not merely reflect low-level visual properties but more high-level perceptual processes for generic face structure.

2.2.2 Individual face recognition/ N250r

Face perception is followed by the recognition of a known face. Repetitions of the same relative to two different individual faces have been shown to elicit enhanced negativities at

occipito-temporal electrodes in the 230-330 ms time window, the N250r (r for 'repetition'; e.g., Begleiter, Porjesz, & Wang, 1995; Schweinberger et al., 1995). This component typically emerges between 180 and 220 ms with a peak at ~250 ms and is elicited bilaterally but is usually larger over the right hemisphere. N250r scalp topographies are characterized by an occipito-temporal negativity at posterior electrodes, which is accompanied by a frontocentral positivity. The sensitivity of this component to repetitions of the same relative to two different faces suggests that this component reflects neural processes that code fine-grained information about face structure that are essential for individual face recognition.

In a series of studies, the N250r component has consistently emerged as an electrophysiological marker of the successful match between an on-line face and a stored visual-perceptual representation of that face (e.g., Schweinberger et al., 1995, Schweinberger, Pickering, Jentzsch, Burton, & Kaufmann, 2002a). Event-related brain potential evidence for a response of inferior temporal N250r amplitudes are typically larger to repetitions of familiar faces than to unfamiliar faces including famous celebrities (Begleiter et al., 1995) or personally familiar faces (Herzmann, Schweinberger, Sommer, & Jentzsch, 2004). Even though unfamiliar faces also elicit N250r effects in immediate repetition paradigms (Itier & Taylor, 2004), these effects tend to be smaller and more transient as reflected by the absence of an N250r when faces intervene between repetitions of two unfamiliar faces (Pfütze, Sommer, & Schweinberger, 2002). These findings suggest that the N250r component indexes face familiarity.

A similar right temporal N250 component has been shown to be triggered to the first presentation of a familiar face. Tanaka, Curran, Porterfield, and Collins (2006) measured N250 amplitudes to target faces as well as participants' own faces. Clear N250 components were elicited from the start to the familiar own face. In contrast, an N250 to the target face was absent during the first experimental half, but emerged during the second half of the experiment when targets faces had become visually familiar. These findings suggest that the N250 reflects the acquisition of both acquired and pre-existing representations for individual faces as a result of face learning. Along similar lines, Kaufmann, Schweinberger, and Burton (2009) showed that an N250 emerged to repetitions of the same unfamiliar face after a learning phase, and this was the case even though different images were used between learning and subsequent recognition. The observation that N250 and N250r show very similar onset latencies and scalp topographies suggests that they reflect the same underlying neural

processes. Therefore, the N250/N250r has been linked to two types of face memory: The N250/ N250r to familiar faces reflects the activation of pre-existing face representations in long-term memory whereas the N250r to unfamiliar faces reflects the match between an incoming face and a short-term face memory trace of that individual acquired during the first encounter (Schweinberger & Burton, 2003).

In the context of the face specificity debate, the question arises whether N250/N250r components are exclusively triggered by human faces. Schweinberger, Huddy, and Burton (2004) tested the face selectivity of the N250r, and found that repetitions of human faces elicited significantly larger N250r negativities at occipito-temporal electrodes relative to inverted faces or cars. Figure 2.2 shows N250r scalp topographies obtained in response to different types of stimuli, highlighting the prominent N250r for human faces over inferior occipito-temporal regions, a similar but smaller effect for ape faces, and the absence of any such effect for cars.

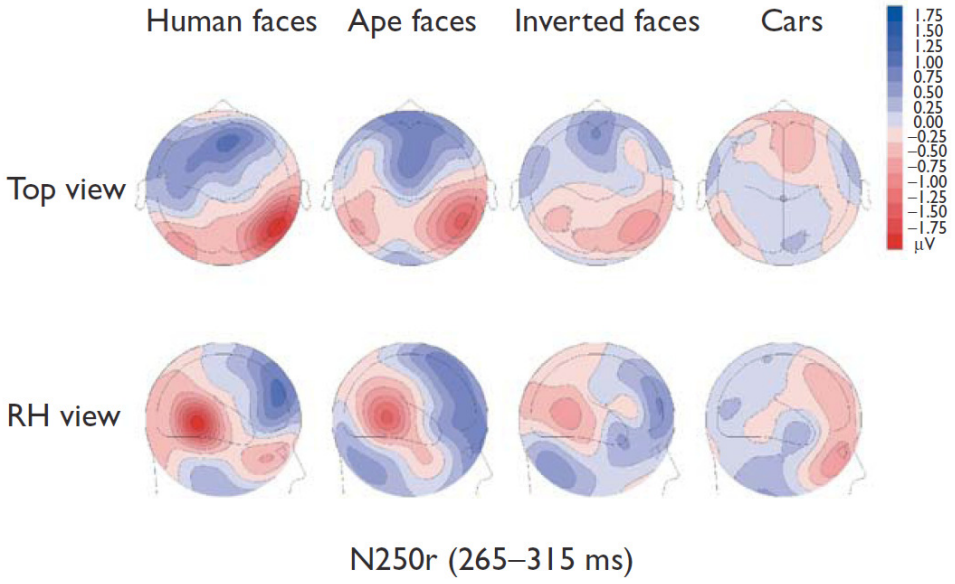


Figure 2.2 Scalp topography of the N250r ERP component for different types of stimuli. Depicted is the ERP difference between repeated and unrepeated stimuli for four categories including famous human faces (Schweinberger et al., 2004). Note that enhanced negativities are shown in red, enhanced positivities in blue.

While findings from Schweinberger et al. (2004) demonstrate that the N250r response is characterized by a degree of face selectivity, evidence has started to emerge which suggests that the N250 is, to some extent, modulated by perceptual expertise. In a study by Scott, Tanaka, Sheinberg, and Curran (2006), participants were trained to discriminate images of

wading birds or owls at either the basic category level (e.g., owl) or at an individual species level (e.g., snowy owl). Enhanced N250 amplitudes were found only to those stimuli that had been learned at the individual level (as compared to the basic level), suggesting that this component reflects the acquisition of perceptual expertise in discriminating individual exemplars. These findings suggest that N250 components are elicited to objects of visual expertise, and are therefore not exclusive to faces. However, faces were not studied in the Scott et al. study, so differences in the functional properties between 'face' and 'object' N250 could not be assessed. Others (e.g., Tanaka & Pierce, 2009) also reported an increased N250 component as a result of extensive training in individuating other-race faces at the subordinate-level (e.g., Joe), which they referred to as the 'expert N250'. Overall, these results suggest that the N250/ N250r reflects a degree of face specificity, but is (to some extent) modulated by perceptual expertise.

An interesting question about the functional properties of the N250/N250r concerns whether this component reflects the perception of unique identity above and beyond purely perceptual information. Past research suggests a degree of (but not complete) image-independence of the neural processes that give rise to the N250r component. Caharel et al. (2009) showed that a reliable N250r was triggered by repetitions of the same unfamiliar face shown from different views. In this study, the first face on each trial was shown in a full front view while the second face was always oriented 30° to the right. The finding of a prominent N250r over posterior electrodes to repetitions of the same relative to two different individuals irrespective of the view change suggests that this component reflects a degree of view-invariant identity processing, even when faces are unfamiliar. This is further supported by findings that the N250r to same face repetitions generalizes across geometrically altered unfamiliar faces (Bindemann, Burton, Leuthold, & Schweinberger, 2008) or different images of famous celebrities (Schweinberger et al., 2002a). However, in Schweinberger et al.'s study, N250r amplitudes were larger to identical image repetitions as compared to repetitions of two different images of the same famous celebrity, suggesting that it reflects flexible identity-specific face processes but no complete independence from low-level visual cues.

Overall, the studies reviewed suggest that N250/N250r components represent a likely neural correlate for Bruce and Young's 'face recognition units' or FRUs representing high-level abstract representations of individual faces. The neural generators of the N250/ N250r component have been linked to face-selective activity in the lateral fusiform gyrus (FG),

including the FFA, which has been associated with the perception of unique identity (Schweinberger et al., 2002a). This is further in line with activation in fusiform face regions to repeated presentations of individual faces in fMRI studies (Eger et al., 2005). Moreover, a recent study (Gosling & Eimer, 2011) demonstrated that the N250 component is only triggered by famous faces that are judged as definitely known relative to famous faces that merely appear familiar, indicating that the N250 indexes neural processes that underlie the explicit identification of a familiar face.

In conclusion, the present ERP data indicate that the occipito-temporal N250/N250r component indexes early perceptual face processing stages where identity-specific information about faces is extracted that can be re-activated when the same individual is repeated. These visual face memory traces for individual faces can be based either on pre-existing representations in long-term memory or newly acquired representations to unfamiliar faces in short-term memory. Therefore, N250/N250r components reflect two different types of recognition memory depending on the familiarity with a particular face whereas the size of this component indexes the level of familiarity with a particular face.

2.3 Repetition priming

Important insights into cognitive processes have been obtained by investigating behavioural or neural responses to repeated presentations of the same stimulus. Processing a visual stimulus is improved by prior perceptual experience with that stimulus, a phenomenon called 'priming'. Perceptual priming is reflected by greater accuracy and/or faster response times in identifying repeatedly presented as compared to novel stimuli (e.g., Tulving & Schacter, 1990). The more efficient processing of a previously seen ('primed') stimulus has been linked to the re-activation of the same neural processes to the repeated stimulus. A distinction has been made between tasks in which processing of both first and repeated presentation of a stimulus is required, and tasks that require only explicit processing of the second stimulus although processing of the first stimulus may occur implicitly (Schacter, & Buckner, 1998). The former type of task is termed direct or explicit, whereas the latter is termed indirect or implicit. Even though, repetition effects are observed in both implicit and explicit tasks, the underlying memory processes appear to be dissociable. Strong evidence for such a functional distinction comes from amnesic patients who show perceptual priming effects despite severe impairments on explicit memory tests (Hamann & Squire, 1997).

Importantly, even though repetition-priming effects are strongest to repetitions of identical stimuli, facilitated processing is also observed when non-identical but related stimuli are repeated, such as different images of the same stimulus, suggesting that the underlying neural mechanisms generalise across low-level image-based properties (e.g., Ellis, Young, Flude, & Hay, 1987).

2.3.1 The neural basis of priming

Repetition modulations are not only observed in behaviour, but are also reflected by changes in neural responses using electrophysiological or neuroimaging methods (Grill-Spector, Henson, & Martin, 2006). The most common finding across different experimental paradigms is a reduction in neural activity to repeatedly presented stimuli. Single-cell recordings in non-human primates have shown that neurons in the ventral temporal lobe reduce their firing pattern to the second presentation of a stimulus relative to the presentation of novel items (Baylis & Rolls, 1987). This is further supported by functional brain imaging studies in humans (e.g., Grill-Spector et al., 1999; Henson, 2003). These showed a reduction in the fMRI signal to repeated stimuli, a phenomenon known as 'repetition suppression' (Desimone, 1996) or 'adaptation' (Grill-Spector & Malach, 2001). To account for the reduced neural responses associated with stimulus repetition, three models have been suggested. Firstly, the Fatigue model, according to which firing rates of stimulus-selective neurons decrease in amplitude to repeated presentations (referred to as "neural fatigue") resulting in greater neural synchrony. Secondly, the Sharpening model, according to which repetition suppression reflects sparser neural representation of stimuli thereby "sharpening" the selectivity of the neural response. According to this view, despite a global decrease in neural firing, stimulus-specific neurons increase their firing rates resulting in more efficient or faster processing of repeated stimuli. And thirdly, the Facilitation model, according to which a decrease in neural activity reflects shorter latencies or durations of neural firing, and therefore a faster processing stream of repeated information through the brain (Grill-Spector et al., 2006). It is plausible that each model accounts for repetition-related neural responses at different time scales. For instance, immediate repetition effects may be best explained by 'neural fatigue', reflecting transient neural changes. In contrast, long-lag repetition effects may indicate stable changes associated with long-term learning as a result of 'sharpening' of stimulus representations.

Repetition paradigms in psychological research are based on the rationale that if neural responses decrease following repeated stimulus presentations, then the associated region is involved in the processing of that stimulus. Similarly, if a reduction in neural activity is observed across stimulus-related changes, then this region is invariant to that stimulus property. Even though repetition effects are typically associated with reductions in neural activity, enhanced responses to repeated stimuli have also been observed referred to as 'repetition enhancement'. For example, Miller and Desimone (1996) reported that a particular neural population in monkey cortex shows an enhanced neural response to stimulus repetitions. Similar enhancements in neural activity have also been observed in human fusiform face regions (Henson, Shallice, & Dolan, 2000). This repetition-related boost in neural activity may reflect the recruitment of additional brain regions in response to the repeated stimulus, presumably reflecting the re-activation of visual memory representations of the first encounter with a stimulus. This would suggest that a decrease in neural activity is observed when two stimuli engage the same low-level visual processes while enhanced neural responses index the recruitment of higher-level memory-related processes. Moreover, neural response properties to stimulus repetitions appear to be modulated by several factors such as the time lag between repetitions, or the particular brain region (Fang, Murray, & He, 2007).

Taken together, repetition paradigms represent a highly useful tool for identifying and localizing stimulus-specific neural processes that show facilitated processing of a repeated stimulus as a result of prior experience. Two types of neural responses have been observed for stimulus repetitions: repetition suppression or repetition enhancement. A reduction in neural activity is thought to occur when both initial and repeated stimulus activate the same underlying neural processes. In contrast, an increase in the neural response to stimulus repetitions has been attributed to the additional recruitment of memory-related brain regions in response to the repeated stimulus.

2.3.2 Repetition priming in face recognition

Repetition paradigms have emerged as a useful tool for studying face-selectivity in the human brain. Facilitated face recognition following priming has been shown for several stages of human face perception such as the identification of familiar faces (Bruce & Valentine, 1985; Ellis et al., 1987). These priming studies have shown that prior exposure to a famous

face or retrieval of a person's name facilitates subsequent face recognition. Under very short stimulus onset asynchronies, inter-modal repetition priming effects have also been reported where hearing voices of a familiar face facilitated subsequent identification of that face (Ellis, Jones, & Mosdell, 1997). Ellis, Flude, Young, and Burton (1996) propose two different loci for priming effects in familiar face recognition. The first involves the perceptual analysis of a familiar face whereas the second includes the activation of semantic information, which is facilitated by both within-domain (i.e. semantic) and across-domain (i.e. perceptual) priming.

Several neuroimaging studies have reported reduced fMRI responses to the second as compared to the first presentation of a face (e.g., Henson et al., 2000; Kanwisher et al., 1997). For example, repeated exposure to well known, famous faces produced attenuated responses in the fusiform gyrus (Henson, Shallice, Gorno-Tempini, & Dolan, 2002). Repetition suppression effects for familiar faces have been attributed to the activation of pre-existing perceptual representations in contrast to repetition enhancement for repeated presentations of unfamiliar faces (Henson et al., 2002). In line with behavioural priming effects, adaptation effects in core face-selective regions are strongest for identical-image repetitions, but also emerge for repetitions of the same familiar person shown from different viewpoints (Eger et al., 2005). These findings support the view that a more abstract representation of facial identity is processed in fusiform face regions. In addition, fMRI repetition suppression is influenced by task demands where greater suppression effects are found when subjects are making decisions related to facial identity (i.e., famous/ nonfamous judgments) as compared to identity-unrelated tasks (Henson et al., 2002).

Distinct ERP modulations have also been shown for repeatedly presented individual faces (e.g., Eimer et al., 2000a; Schweinberger et al., 1995). The most consistent finding across different paradigms is that repeated faces evoke a reduction in the face-sensitive N170 component in the 160-190 ms post-stimulus time interval. These N170 adaptation effects have been observed for a variety of face or face-like stimuli during the holistic-configural analysis of faces prior to face identification (Eimer et al., 2000d; Caharel et al., 2009). While early face-selective N170 components are characterized by a reduction in the neural response to face repetitions, the subsequent N250r response to face repetitions shows an enhanced neural response to repetitions of the same face (e.g., Schweinberger, Pickering, Burton, & Kaufmann, 2002b). This repetition-related boost is thought to index the re-activation of pre-existing or newly acquired face representations in visual memory. The N250r can reflect

either the activation of short-term memory traces for unfamiliar faces, or robust long-term memory representations for familiar faces. Increases in N250r amplitudes to repeated presentations of the same (or a different) image of the same person are thus thought to reflect the additional engagement of face memory processes acquired to the first presentation of that face. Therefore, while the N170 indexes the early perception of face structure, the N250r reflects access to memory representations of individual faces.

In summary, studying ERP modulations to repeated presentations of faces provides important insights into distinct neural processes that are involved in the perception of different types of information from faces. In particular, the finding of a reduction in the ERP response during early face perception as compared to a neural increase during explicit face recognition highlights the point in time where memory representations of individual faces are retrieved. Therefore, differences in functional properties of ERP responses indicate the sequential nature of distinct face processing stages, and their temporal dynamics.

2.4 The present thesis

The present thesis is an investigation of the processes and mechanisms that underlie the perception and memory representation of individual unfamiliar faces. As highlighted in Section 1.4, relatively little research has focused on the neural basis of unfamiliar face recognition, and most importantly whether (and how) neural systems for the perception of familiar and unfamiliar faces differ. Previous research has raised several open questions: What type of information is encoded from an unfamiliar face? Are visual memory traces of unfamiliar faces based on low-level *pictorial* (i.e., view-dependent) or more abstract *structural* (i.e., view-independent) information? The second research question concerns the roles of task-set dependent attention (i.e., strategic processing) and visual working memory (WM) in face identity processing. Are identity-specific visual cues processed in an optional (i.e., task-dependent) or an obligatory fashion? A final research aim was to investigate the neural basis of face identity processing in developmental prosopagnosia (DP). Behavioural and ERP measures were used in the present thesis in order to address these questions. The first two studies (Experiments 1 & 2) investigated the view-dependence or independence of unfamiliar face recognition, and the impact of face learning on visual face recognition processes. A second series of four studies investigated the influence of strategic processing (Experiments 3-5) and WM decay (Experiment 6) on identity-related face processing. A final

study (Experiment 7) investigated the nature of face recognition impairments in individuals with developmental prosopagnosia (DP). The aims and rationale of these experiments will be outlined below.

2.4.1 View-independent recognition and face learning

As outlined in Chapter 1, a functional distinction between familiar and unfamiliar face recognition has been proposed where the former is based on high-level structural information and the latter on low-level pictorial information about individual facial identity. In Chapters 3 and 4, two experiments will be described that investigated what type of visual information is processed from an unfamiliar face when the same individual is repeated in a different view. Experiment 1 tested the view-dependence or independence of unfamiliar face recognition processes across view changes on each trial. If the N250r is view-independent, this component should generalize across changes in viewpoint, and varying degrees of rotations. To investigate the impact of learning on visual face recognition processes, Experiment 2 compared N250r amplitudes to initially novel unfamiliar faces and experimentally familiarized faces. If face learning changes the perceptual mechanisms of unfamiliar face recognition, a qualitative shift from view-dependent to view-independent recognition should emerge when novel faces become more familiar.

2.4.2 The roles of attention and WM in face identity processing

A series of three studies (Experiments 3-5) that investigate the influence of strategic processing (i.e., task-dependent attention) will be presented in Chapters 5-6. The first two experiments studied whether information about facial identity is processed in an optional or obligatory fashion in *implicit* tasks where identity is task-irrelevant. In Experiment 3, participants performed an *implicit view*-matching task requiring same/different view judgments. Even though facial identity is irrelevant, participants need to actively maintain a visual memory trace of the view (but not the identity) of the first face, and identity-specific facial cues may be encoded in an obligatory fashion. In Experiments 4 and 5, ERP markers of identity recognition were compared during two tasks: face identity matching (*explicit*) or target detection (*implicit*). The explicit task involves the formation of a face memory trace, while the implicit task does not have this memory component, but requires immediate response to inverted face targets. While unfamiliar faces were used in Experiment 4, images of famous celebrities and non-famous faces were presented in Experiment 5. If task-

dependent attention is required for the acquisition of a perceptual memory trace of an individual's identity, differences in identity-sensitive N250r responses should be observed for *explicit* and *implicit* tasks. The sixth study (Experiment 6) described in Chapter 7 studied the persistence of perceptual face memories in visual working memory (WM) over short periods of time. If the strength of newly acquired perceptual face representations is affected by the time interval between repetitions of the same face, a decrease in the strength of these representations should be observed with longer repetition intervals.

2.4.3 Face identity processing in DP

In addition to studying face perception in adults with typical face recognition abilities, the final experiment (Experiment 7 described in Chapter 8) investigated the neural basis of face recognition impairments in individuals with developmental prosopagnosia (DP). In particular, the presence and nature of *implicit* face identity processing was studied in a group of DP participants to repetitions of unfamiliar face pairs. DP and control participants performed a view-matching task, where facial identity is processed in a mandatory fashion in adults with typical face recognition abilities. If DP can be caused by selective impairments during post-perceptual face processing stages, early perceptual stages of face identity processing should be, to some extent, intact in DP, mirroring those observed in control participants.

Chapter 3. Perceptual mechanisms of unfamiliar face recognition

Past research into the neural basis of unfamiliar face processing has left several open questions about the type of visual cues that are extracted from an unfamiliar face (i.e., pictorial versus structural; see Bruce & Young, 1986). Behavioural and ERP measures were used in the present thesis in order to investigate several open issues. The first two experiments (Experiments 1 and 2) investigated the neural mechanisms that underlie the acquisition of new visual-perceptual face memories. While much research has focused on familiar face recognition, relatively little is known about unfamiliar face recognition and the process by which unfamiliar faces become familiar. In Bruce and Young's model, familiar faces are processed and encoded in a flexible image-invariant fashion by means of abstract identity-related cues (i.e., *structural* codes). Structural codes are stored within face recognition units (FRUs), representing a perceptual storage of unique visual features of a familiar face that distinguish it from other known faces. Furthermore, such high-level codes for facial identity need to be acquired through repeated exposure to the same face across many different encounters, and are not available for strictly unfamiliar (i.e., novel) faces. This view is supported by evidence from recognition memory studies which have shown that pictorial codes dominate the perception and memory representation of unfamiliar (but not familiar) faces, as reflected by the difficulty to identify the same unfamiliar face across image changes such as rotations in viewing angle (Bruce, 1982; Bruce et al., 1999).

The observed behavioural discrepancies between recognition memory for unfamiliar and familiar faces indicate that different neural mechanisms underlie these two types of face recognition (Hancock et al., 2000). But what is their neural basis? Electrophysiological markers represent a useful tool to answer this question, because they allow us to measure the temporal organization and neural basis that underlie early perceptual face recognition processes. Event-related brain potential (ERP) studies of face perception have identified a neural marker elicited by identity repetitions that indexes explicit face recognition (N250r component). The repetition-related N250r is characterized by enhanced negativities to immediate repetitions of two images showing the same as compared to two different individuals (Begleiter et al., 1995; Schweinberger et al., 1995, 2004). An N250r is elicited not only in response to repetitions of familiar faces (i.e., family and friends), but also to experimentally familiarized faces (i.e., initially unfamiliar faces that have become visually familiar in the course of an experiment; see Itier & Taylor, 2004). Due its sensitivity to same

face repetitions, the N250r is thought to index the match between an on-line face image with a stored visual memory trace of that particular individual (Schweinberger & Burton, 2003). These memory representations can either reflect transient and temporarily acquired perceptual face memories based on immediate prior exposure, or permanently stored representations for individual faces in long-term memory. In unfamiliar face repetition paradigms, recognition is based on a visual memory trace that is acquired to the first presentation of a face and is subsequently re-activated when the same face is repeated.

Typically, N250r responses are larger for identical image repetitions, but show a considerable degree of image-independence, and are reliably elicited to repetitions of the same famous individuals shown from two different images (Dörr, Herzmann, & Sommer, 2011; Schweinberger et al., 2002a), as well as to repetitions of the same famous faces across geometrical transformations (Bindemann et al., 2008). This finding is in line with the hypothesis that familiar face recognition is relatively invariant across image transformations. Moreover, an N250r is also reliably triggered to repetitions of unfamiliar faces across different images (Kaufmann et al., 2009) or across caricatures (Schulz, Kaufmann, Walther, & Schweinberger, 2012), indicating a degree of image-invariance during the perception and recognition of not only familiar but also unfamiliar faces. While face memories of highly familiar faces are thought to be based on refined and robust memory representations that have been formed over time, little is known about the mechanisms that underlie the perception of unfamiliar face identity. What type of visual information is extracted from an unfamiliar face? Is unfamiliar face perception and recognition largely based on image-dependent *pictorial* or identity-specific *structural* cues (or a combination of both)? Moreover, do the perceptual mechanisms that underlie unfamiliar face recognition change as initially novel unfamiliar faces become more familiar?

The central research aim of Experiments 1 and 2 was to find out whether unfamiliar face recognition processes, as reflected by the N250r, are based on low-level pictorial or on more abstract view-independent representations. Experiment 1 investigated whether the perception of unfamiliar faces is characterized by view-dependence or independence. Measuring N250r amplitudes to face repetitions that vary along one dimension (e.g., changes in viewpoint) is a suitable method to gain a better understanding into the temporal dynamics of individual face recognition, and the underlying functional properties.

3.1 Experiment 1. Recognizing faces across views: View-dependence or independence

3.1.1 Introduction

Recognizing an unfamiliar face is remarkably easy when two identical images of the same person are shown, yet surprisingly difficult for two different images (e.g., Bruce et al., 1999; Bruce, Henderson, Newman, & Burton, 2001). In contrast, identifying a familiar face across different images or viewpoints is an effortless task (Bruce, 1982), suggesting functional differences in the perception and recognition of familiar as compared to unfamiliar faces. Processing the identity of an unfamiliar face could be achieved by two means: Learning something about the particular image, or learning those unique visual features that define a person's identity. The former refers to the extraction of low-level *pictorial* codes, while the latter requires the acquisition of more abstract *structural* codes. While identical image matching does not require the formation of structural codes, face recognition across different images is thought to involve the formation of an invariant high-level representation for facial identity (Bruce & Young, 1986; but see Longmore, Liu, & Young, 2008). Therefore, it been argued that unfamiliar face recognition is easy and effortless when it is possible to solely rely on pictorial cues, whereas it becomes difficult when different images of the same face are shown, and more abstract codes for facial identity need to be extracted. Those abstract or invariant codes are not available for unfamiliar faces but are thought to emerge once novel faces become familiar. Therefore, same-image matching allows picture recognition (i.e., encoding the exact picture) as compared to identity recognition, which involves learning the identity of faces, and this requires a degree of image-invariance (Bruce & Young, 1986).

Evidence from behavioural studies

The fact that the same individual can look remarkably different in two different photographs poses a serious challenge for face recognition. Most humans are experts in identifying the same familiar face across different images by effortlessly extracting those perceptual cues that define facial identity. In contrast, this task is surprisingly difficult for unfamiliar faces. While image changes can alter the low-level visual features of a face drastically, the overall face configuration stays the same. Contrary to the general view, our "expertise" with faces only applies to the identification of familiar faces, and contrasts with

our poor recognition memory for unfamiliar faces (e.g., see Burton & Jenkins, 2011, for a review). This is illustrated in face-matching studies (e.g., Bruce et al., 1999, 2001) where participants' task is to identify an unfamiliar target face among an array of simultaneously shown face photographs. The target face in the array shows a different image of the target individual, and thus differs in low-level visual properties that are specific to the image, whereas information about face structure remains unchanged. Accuracy on this face-matching task is nevertheless surprisingly low, with participants correctly identifying the target face on only 70% of all trials. In contrast, face matching is remarkably easy with two different images of familiar individuals (Burton & Jenkins, 2011), suggesting that qualitative differences underlie the recognition of familiar and unfamiliar faces. The difficulty to extract identity-specific cues across different images when faces are unfamiliar seems to imply that increasing familiarity with a face fundamentally alters face recognition memory. Therefore, the process of face learning by which initially unfamiliar faces gradually become more familiar during repeated encounters with the same face could be an essential perceptual property of human face recognition. In Bruce and Young's (1986) terms, unfamiliar face memory is dominated by pictorial codes – instance-specific representations that capture all visual details of an image – whereas familiar face recognition is mediated by more flexible and abstract structural codes, allowing generalization beyond a specific image. Face learning might therefore reflect the acquisition of structural codes for facial identity, which are stable and invariant across a variety of image changes, including changes in socially relevant facial cues such as facial expression or view and low-level visual cues such as variations in lighting. This would suggest that the ability to dissociate facial cues that define identity (*structural*) and cues that index image-based properties (*pictorial*) forms the basis of effective face recognition.

In social interactions, there is a constant change in the visual appearance of a face, for example due to head movement resulting in different views of the same person. Varying the viewing angle of a face leaves the overall face layout unchanged but alters image-based properties, so that different views of the same face look quite dissimilar. Moreover, changes in face viewpoint markedly reduce the amount of diagnostic facial information that is available for face identification. For example, depth-related information is absent in a front view but becomes to some extent visible in a side view (i.e., at an angle of about 30°-45°). Each viewpoint therefore provides specific yet limited identity-related cues about facial

identity, and rotating the angle of a face occludes or reveals certain facial characteristics. It is therefore the sum of all previously acquired structural codes that are extracted from different views, which form the basis for a refined representation of the identity of a familiar face. Access to such a rich representation of the defining visual features of a familiar face may then result in the observed 'expertise' in recognizing a well-known face across different instances. On the contrary, if identity-specific visual cues have not yet been learned, recognition memory is impaired when the task requires recognizing an unfamiliar face from different viewpoints (e.g., Bruce, 1982; Bruce et al., 1999). In contrast, recognition accuracy for familiar faces remains relatively unchanged for view changes across front and side views (Bruce, 1982). It has to be noted that profile views seems to be an exception, as these also impair recognition memory for familiar faces (e.g., Hill, Schyns, & Akamatsu, 1997), presumably because a large rotation in viewing angle provides the least diagnostic information about identity. There has been some debate in the literature about whether a side or three-quarter view may represent a 'preferred' face view for identifying facial identity and for generalizing to novel views (Troje & Bülthoff, 1996). The argument has been put forward that a rotation by 30°-45° from a full-front view may provide the most flexible kind of identity-specific facial cues, thereby facilitating generalization to novel front or profile views. At present, there is little evidence to support this view, and it may be that the observed recognition advantage is due to the fact that faces shown in a three-quarter view have smaller possible angles through which they can be rotated (Liu & Chaudhuri, 2002; but see also Hill et al., 1997).

In summary, findings from recognition memory experiments suggest that face recognition requires the perceptual ability to dissociate two types of codes: structural codes that convey identity-defining information and pictorial codes that represent image-based visual cues. While we make this distinction expertly when encountering a familiar face our ability to recognize unfamiliar faces can be surprisingly poor. In particular, changes in face viewpoint alter the amount of diagnostic facial information available for recognition, resulting in the difficulty to match unfamiliar faces across different views. In contrast, the recognition of familiar faces remains relatively invariant across changes of low-level image-based properties, including rotations in the view in which a face is seen.

A neural response to invariant aspects of faces

Having outlined the cognitive mechanisms that are thought to be involved in the perception of individual identity, what are their underlying neural substrates? Evidence from macaques suggests the existence of face-selective neurons in ventral visual cortex, which respond maximally to a particular identity, even when shown from different viewing angles (Desimone, Albright, Gross, & Bruce, 1984; Rolls, 2000), indicating a view-invariant representation of faces at the neural level. Findings from human neuroimaging studies have identified a cortical region in fusiform gyrus that responds selectively to faces relative to other visual objects, referred to as the fusiform face area (FFA; Kanwisher et al., 1997). The FFA is thought to play a major role in the perception and recognition of individual faces (Gauthier et al., 2000b; Grill-Spector et al., 2004). Moreover, neural activity in the FFA has been shown to correlate with face perception during the presentation of ambiguous stimuli (when these were perceived as faces) and even mental imagery (Ishai, Haxby, & Ungerleider, 2002). Therefore, the fusiform face area in humans appears to be involved in the formation of an invariant representation of an individual's face that can be used for recognition (Haxby, Hoffman, & Gobbini, 2002). In contrast, changes in facial cues that are important for social communication, such as expression or gaze, and which are shared across many different identities, elicited the largest neural response in the right superior temporal sulcus (rSTS; Allison et al., 2000; Haxby et al., 2000). Thus, STS as well as the amygdala might be important for processing changing or dynamic features in faces whereas the FFA is involved in the visual analysis of invariant aspects of faces (i.e., identity). This would indicate a functional selectivity in distinct regions in the fusiform gyrus, even though processing in these regions may not be entirely encapsulated and independent (Vuilleumier et al., 2001).

Even though the FFA has consistently been shown to process identity-specific facial cues (Gauthier et al., 2000b; Grill-Spector et al., 2004), it remains unclear how identity is represented in the FFA. To address this question, a series of neuroimaging studies has used repetition-priming paradigms to study whether (and where in the brain) familiar and unfamiliar face representations are view-dependent or independent. Repetition priming leads to decreased neural activation for repeated stimuli as compared with their initial presentation, reflecting a selective adaptation of neurons tuned to particular stimulus attributes when these attributes are repeated (Grill-Spector & Malach, 2001). A review of the fMRI literature indicates that most research has shown that the FFA adapts to repetitions of

the same unfamiliar face when shown in the same view, but recovers when the viewpoint of the face is changed (Andrews & Ewbank, 2004; Pourtois, Schwartz, Seghier, Lazeyras, & Vuilleumier, 2005a). Pourtois et al. (2005a) presented pairs of unfamiliar faces of which the first face was either shown in a front or side view, and either repeated with the same view (using two different images) or with a different view. Neural responses in the FFA demonstrated the view-dependence of unfamiliar face recognition, with a partial generalization on trials where a front view was followed by a side view, but not for the reverse condition (i.e., a side view followed by a front view). While this indicates that representations of unfamiliar in the FFA are not fully view-independent, more medial regions in the fusiform cortex showed reduced neural responses to same face repetitions across all types of view changes. These regions were outside but adjacent to the face-selective FFA, and may be involved in more abstract or semantic representations of individual faces. A second study (Pourtois, Schwartz, Seghier, Lazeyras, & Vuilleumier, 2005b) compared face-selective adaptation effects across changes in viewpoint using both unfamiliar and famous faces. There was no reduction in the FFA across view changes even for repetitions of famous faces that have repeatedly been seen across different images and different viewpoints. Taken together, these findings do not support the hypothesis that the FFA represents faces in a strictly view-independent format, even though some degree of generalization across image variability, including certain changes in face view, have been observed.

At present, there is little evidence for qualitative differences in neural responses to familiar as compared to unfamiliar faces (see Natu & O'Toole, 2011, for a review). However, Ewbank and Andrews (2008) provided evidence that the FFA may dissociate between familiar and unfamiliar face perception: Activity in the FFA was reduced when faces of the same individual were repeated, and this effect was modulated by familiarity. Neural adaptation was view-dependent for unfamiliar faces but view-independent for familiar faces. These results provide a neural basis for differences in the recognition of familiar and unfamiliar faces. Along similar lines, Eger et al. (2005) reported differences in the degree of image dependency across fusiform cortex. Stronger image-dependence was found in right than left anterior fusiform gyrus. Additionally, greater generalization across different images was observed in anterior as compared to middle fusiform cortex, but only for familiar faces, suggesting that representations become increasingly more abstract along the hierarchy of the ventral visual

pathway. These findings emphasize that familiarity with a face enhances the invariance of the underlying neural representation.

In contrast to the reviewed neuroimaging evidence, findings from electrophysiological research present a different picture: A considerable degree of image-independence of familiar face recognition is suggested by the fact that the identity-sensitive N250r component is reliably present over occipito-temporal regions to repetitions of the same famous individual shown across different images (Schweinberger et al., 2002a) or geometric distortions (i.e., vertically or horizontally stretched images; Bindemann et al., 2008). However, the observed amplitude modulations for different-image as compared to same-image repetitions indicate that the N250r response is not fully image-invariant (Schweinberger et al., 2002a). Evidence for robust coding of visual cues for facial identity has also been shown for repetitions of unfamiliar faces where an N250r is reliably present across different photographs (Kaufmann et al., 2008) or changes in view (i.e., front or side views; see Caharel et al., 2009). In the Caharel et al. study, the first face on each trial was always shown in a full front view while the second face was shown in a side view. The presence of a clear N250r to repetitions of the same unfamiliar face despite changes in viewpoint on each trial demonstrates that this component generalises across perceptual changes, even when faces are unfamiliar.

Taken together, in spite of clear behavioural discrepancies between familiar and unfamiliar face recognition, there is little systematic insight into the neural basis of these differences. This includes the question whether invariant perception of facial identity over and above image properties does involve the FFA. While most fMRI research indicates that viewpoint-specific representations underlie both unfamiliar and familiar face recognition in the FFA, ERP evidence suggests a degree of invariant coding of facial identity in fusiform face regions.

Research aims

Experiment 1 investigated whether rapidly generated visual memory traces for unfamiliar faces are characterized by view-dependence or independence. N250r components were recorded to pairs of sequentially presented unfamiliar faces that were presented at fixation. Faces were shown in either a full-front, side or profile view, and view always changed between repeated faces of the same individual. On half of all trials, two images showed the same person. In the other half, two different individuals were shown. To go beyond previous research, changes in viewpoint could be either 45° or 90° (small versus large) to investigate

whether N250r components generalize across large changes in view. Participants performed a face-identity matching task, and reported on each trial whether the same or two different individuals were presented. Unlike previous experiments, a rapid repetition paradigm was employed where two faces were presented for 200 ms each, separated by a 200 ms interstimulus interval (ISI) to test whether N250r responses are elicited by very rapid stimuli repetitions. Two hypotheses were tested: First, if the N250r reflects a high-level structural face representation, this component should generalize across repetitions of the same face shown in two different views. Second, if N250r amplitudes are unaffected by the degree of angular rotation (45° versus 90°: small versus large), this would provide strong evidence for the view-independence of the underlying face recognition processes.

3.1.2 Method

Participants

Fifteen volunteers (ten females), aged 22 to 30 years (mean age 26 years, SD = 2) were tested. Data from three further participants were excluded due to an insufficient number of artifact-free EEG trials (less than 60% of all trials left after artifact rejection), excessive alpha activity, or an inability to perform the task. All participants were right-handed, had normal or corrected-to-normal vision, and gave written informed consent prior to testing.

Stimuli and procedure

The stimuli set consisted of 12 unfamiliar faces (six female faces) created using FaceGen Modeller 3.4 (Singular Inversions Inc., Toronto), with which participants were already familiarized (i.e., the same set of stimuli had been used in a previous pilot study). Faces were full-colour images, and were shown either in a front view, a left-facing side view at a viewing angle of approximately 45° and a left-facing profile view at an angle of 90° (see Figure 3.1, bottom panel). All images were cropped into an oval shape using Adobe Photoshop 6.0 (Adobe Systems Inc.). Face images subtended a visual angle of 7.3° × 5.3°. The combination of 12 different identities and three different views resulted in a total of 36 face images. All face stimuli were presented centrally on a CRT monitor against a dark grey background (0.3 cd/m^2), at a viewing distance of 100 cm, using E-Prime software (Psychology Software Tools, Pittsburgh, PA). Their average luminance was 19.4 cd/m^2.

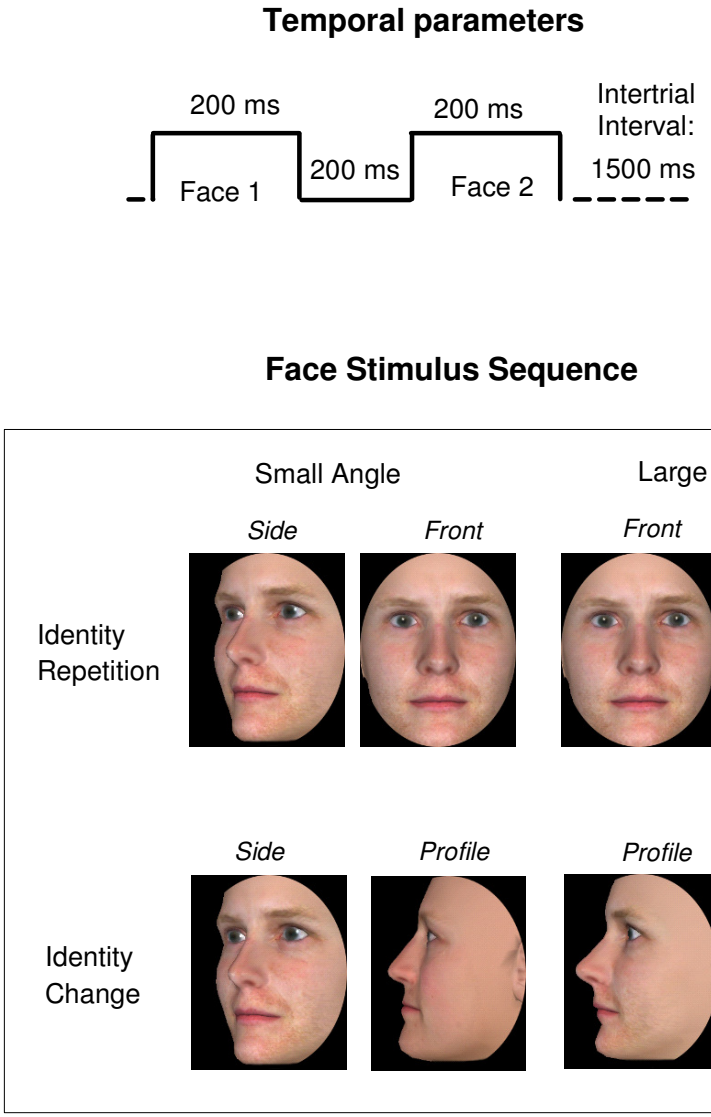


Figure 3.1 Top panel: Temporal parameters of stimulus presentation on each trial. Bottom panel: Examples of the four different face stimulus sequences. On each trial, two faces showed either the same or two different identities (identity-repetition versus identity-change). Face view changed on each trial, and the angular rotation could either be 45° or 90° (small versus large angle).

On each trial, two faces were presented in rapid succession for 200 ms each, separated by a 200 ms inter-stimulus interval (see Figure 3.1, top panel). The inter trial-interval was 1500 ms. Two faces showed either the same or two different individuals, and view always changed between first and second stimulus. For the purpose of analysis, the angular difference between first and repeated face view in each stimulus pair had two levels: 45° versus 90°

(small versus large). For example, a face that was first shown in a front view and repeated in a profile view had an angular change of 90°. This resulted in two types of rotations: small rotations (collapsed across side-front and side-profile) and large rotations (collapsed across front-profile and profile-front). Eight experimental blocks of 80 trials were run with self-paced breaks. Forty trials per block (10 for each of the four combination of face view: side-front, side-profile, front-profile, or profile-front trials) included faces of two different individuals. In the other 40 trials, the same individual was shown.

The view of the second face (i.e., either front or profile view) remained constant within each experimental block, and alternated across successive blocks. Six participants started with a block where the second face was always presented in a front view, and the other six started with a profile-view block. Participants performed an identity-matching task and responded with a left-hand button press on identity repetition trials (regardless of the view in which the two faces were shown), and with a right-hand button press on identity change trials. The experiment lasted approximately 25 min, and participants performed two training blocks (one where the second face showed a front view, and one were it showed a profile view) prior to testing.

EEG recording and data analysis

EEG was DC-recorded with a BrainAmps DC amplifier (upper cut-off frequency 40Hz, 500 Hz sampling rating) and Ag-AgCI electrodes mounted on an elastic cap from 23 scalp sites Fpz, F7, F3, Fz, F4, F8, FC5, FC6, T7, C3, Cz, C4, T8, CP5, CP6, P7, P3, Pz, P4, P8, PO7, PO8, and Oz, according to the extended international 10-20 system). Horizontal electrooculogram (HEOG) was recorded bipolarly from the outer canthi of both eyes. An electrode placed on the left earlobe served as reference for online recording, and EEG was re-referenced off-line to the average of the left and right earlobe. Electrode impedances were kept below 5 kΩ. No additional off-line filters were applied. For each EEG epoch, amplitude values were computed relative to a baseline with a duration of 100 ms (ranging from 50 ms before to 50 ms after the onset of the second face stimulus). Epochs with activity exceeding ±30 μV in the HEOG channel (reflecting horizontal eye movements) or ±60 μV at Fpz (indicating eye blinks or vertical eye movements) were excluded from analysis, as were epochs with voltages exceeding ±80 μV at any other electrode. Following artifact rejection, EEG waveforms were

averaged separately for factors identity (identity-repetition versus identity-change) and angle of rotation (small versus large).

Mean amplitude values were computed at posterior electrodes P7/8 for the N170 time interval (160-190 ms after the onset of the second face) and for the N250r time interval (250-300 ms after the onset of the second face where the effect was maximal). Analogous analyses were also computed for frontal electrode Fz. Repeated-measures analyses of variance (ANOVAs) were performed for factors identity (identity-repetition versus identity-change), angle (45° versus 90°: small versus large) and hemisphere (left versus right: P7 versus P8). Additional analyses were performed for four-level factor view condition (i.e., side-front, side-profile, front-profile, or profile-front), and experimental half (blocks 1-4 versus blocks 5-8). EEG data were analysed for correct trials only.

3.1.3 Results

Behaviour

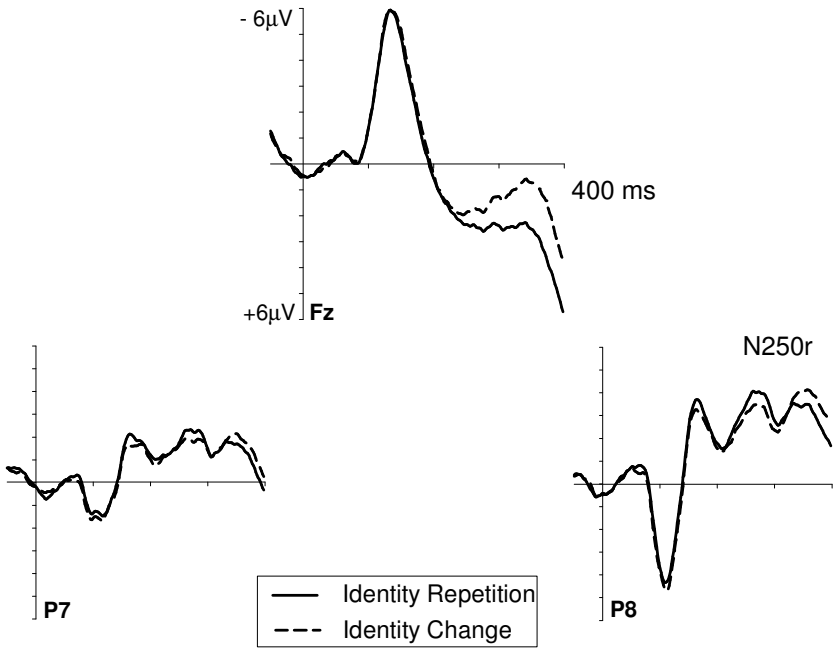
Participants correctly matched the identity of face pairs on 80% of all trials. There was no main effect of identity (81% versus 80% correct for identity repetitions versus changes; $F < 1$). A main effect of angle reflected higher accuracy on trials with a small relative to a large angle (84% versus 77%; $F(1,14) = 17.2$; $p < .01$), but there was no interaction between identity and angle ($F(1,14) = 2.3$; $p = .151$). Accuracy was higher in the second half of the experiment as compared to the first half, but this effect was not significant (82% versus 80%; $F(1,14) = 3.9$; $p < .07$). An interaction between identity and half was not significant ($F(1,14) = 4.1$; $p < .07$), and separate follow-up analyses revealed no significant main effects of identity for either first or second half (both $F < 1$). There was no three-way interaction (identity x angle x half: $F(1,14) = 2.5$; $p = .138$).

Mean correct RT was 639 ms. There was a trend for participants to respond faster on identity-repetition than on identity-change trials but this difference was not significant (633 ms versus 642 ms; $F < 1$). RTs were significantly faster on trials with small versus large angles of rotation (624 ms versus 652 ms; $F(1,14) = 14$; $p < .01$). There was no interaction between identity and angle ($F(1,14) = 2.3$; $p = .149$). RTs were faster in the second half as compared to the first half (616 ms versus 659 ms; $F(1,14) = 11.7$; $p < .01$), but there was no interaction between identity and half, or a three-way interaction (identity x angle x half; both $F < 2$).

Separate analyses for the factor view condition (i.e., side-front, side-profile, front-profile, or profile-front) showed a significant main effect of view condition ($F(3,42) = 12.4$; $p < .01$), demonstrating that participants were most accurate on side-front trials (86%) relative to side-profile, profile-front and front-profile (82%, 78% and 77%, respectively). A significant interaction between identity and view condition ($F(3,42) = 4$; $p < .03$) was followed up with paired t-tests. These confirmed a main effect of identity for side-front trials (91% versus 81% for identity repetitions versus changes; $t(14) = 3.6$; $p < .01$). In contrast, there were no main effects of identity for any of the other three view conditions (all $t < 1$). For RT, there was again a main effect of view condition ($F(3,42) = 8.5$; $p < .01$), demonstrating that RTs were fastest for side-front trials (606 ms) as compared to side-profile, profile-front and front-profile trials (641 ms, 651 ms and 653 ms, respectively). A significant interaction between identity and view condition was obtained ($F(3,42) = 6.8$; $p < .01$). Follow-up analyses revealed a main effect of identity for side-front trials (585 ms versus 627 ms for identity repetitions versus changes; $t(14) = 2.5$; $p < .03$), but no main effects of identity for any of the other three view conditions (all $t < 2$).

ERP markers of visual face memory

Figure 3.2 (top panel) shows ERP grand averages elicited by identity repetitions versus changes at lateral occipital electrodes P7 and P8 and anterior frontal electrode Fz in the 400 ms interval after the onset of the second face in a pair, collapsed across all experimental blocks. Identity repetitions triggered clear N250r components, reflecting the typical enhanced negativity to two images showing the same as compared to two different identities, in spite of the fact that all repeated faces were shown in different views.



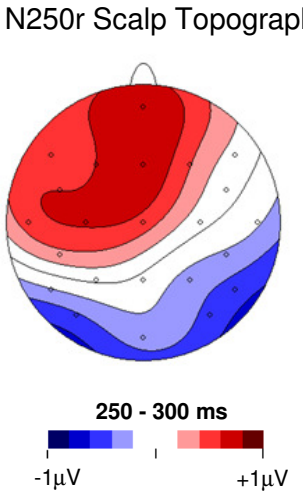


Figure 3.2 Top panel: Grand-averaged ERPs measured at lateral posterior electrode pair P7/8 and frontal electrode Fz for identity-repetitions (solid lines) and identity-changes (dashed lines), collapsed across all trials. Bottom panel: Topographic maps constructed by spherical spline interpolation (Perrrin, Pernier, Bertrand, & Echallier, 1989) of ERP difference amplitudes in the N250r time window (250-300 ms after the onset of the second face) obtained by subtracting ERP mean amplitude on identity-change trials from ERP mean amplitudes on identity-repetition trials. Note that enhanced negativities are now shown in blue, enhanced positivities in red.

Scalp topographies of ERP amplitude differences were calculated separately for identity-repetitions versus changes in the N250r time window (250-300 ms after the onset of the second face; see Figure 3.2, bottom panel). Characteristic bilateral negativities were present over posterior electrodes (N250r components), and these were accompanied by an anterior positivity in the same latency range. Figure 3.3 (top panel) shows ERPs elicited on identity-repetition and identity-change trials, separately for trials with small or large angles of rotation between two faces in a pair. As is evident from the grand averages, very similar N250r components were elicited on trials with both small and large angles of rotation, and these showed the characteristic scalp topographies with a posterior negativity that was accompanied by a frontal positivity (see Figure 3.3., bottom panel).

There was no significant main effect of identity in the N170 time window (160-190 ms after the onset of the second face; $F(1,14) = 3.1$; $p = .101$), confirming that N170 components were unaffected by identity repetitions versus changes. A significant main effect of identity was present in the 250-300 ms N250r time window at posterior electrodes P7/8 ($F(1,14) = 11.2$; $p < .01$), reflecting enhanced negativities to repetitions as compared to changes of identity. There was no interaction between identity and hemisphere ($F(1,14) = 1.8$; $p = .203$), suggesting that N250r components of similar size were elicited in both hemispheres. Follow-up analyses showed a significant main effect of identity at right hemisphere electrode P8 ($F(1,14) = 16.8$; $p < .01$), but this effect did not reach significance at left hemisphere electrode P7 ($F(1,14) = 3.5$; $p < .09$).

The critical question was whether N250r amplitudes would be affected by the degree of angle rotation between the first and the second face in a pair. Statistical analyses showed no significant interaction between identity and angle ($F < 1$), and separate analyses for each level of angle confirmed the presence of a reliable N250r for both small angles of rotation ($F(1,14) = 5.3$; $p < .04$), as well as for large angles of rotation ($F(1,14) = 4.9$; $p < .05$; see Figure 3.3). To test whether the size of the N250r would be differentially modulated by one of the four view conditions, additional analyses were performed on the four-level factor view condition. Results showed a main effect of identity ($F(1,14) = 11.8$; $p < .01$), but no significant interaction between identity and view condition ($F(3,42) = 2$; $p = .135$), indicating that an N250r of similar size was obtained across all four view conditions.

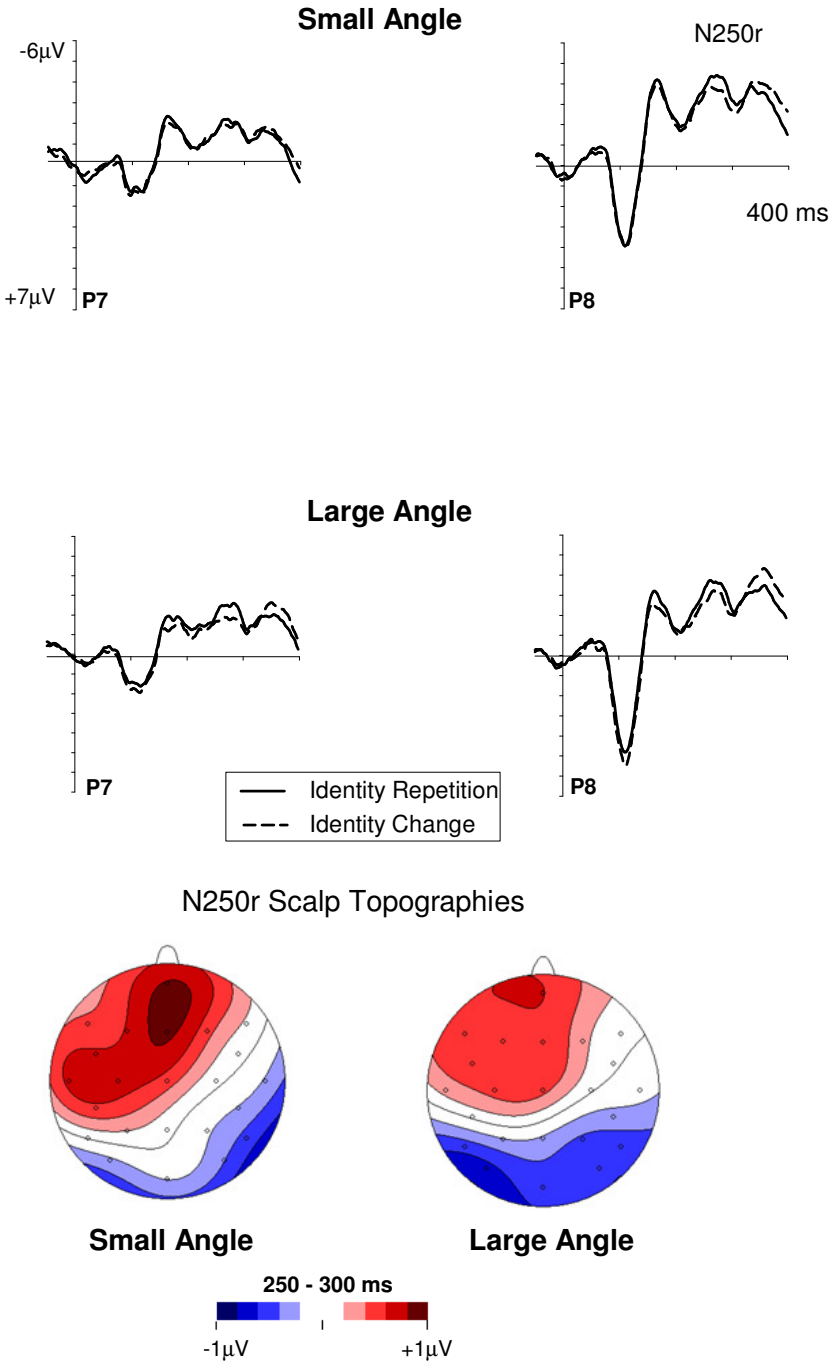


Figure 3.3 Top panel: Grand-averaged ERPs elicited at lateral posterior electrode pair P7/8 in the 400 ms interval after the onset of the second stimulus for identity-repetitions (solid lines), as compared to identity changes (dashed-lines), shown separately for trials with small versus large angles of rotation. Bottom panel: N250r scalp topographies obtained by subtracting ERPs in the 250-300 ms post-stimulus time window on identity-change trials from ERPs on identity-repetition trials.

Analogous analyses were run at frontal electrode Fz in the 250-300 ms time window (frontal positivity). A main effect of identity approached significance ($F(1,14)= 4.2$; $p < .06$), reflecting larger positivities to repetitions as compared to changes of identity. There was no interaction between identity and angle ($F < 1$). Inspection of grand-averaged ERP waveforms showed that this frontal positivity had a delayed onset relative to the posterior N250r, as confirmed by a highly significant main effect of identity in the subsequent 300-350 ms time interval ($F(1,14) = 10.3$; $p < .01$). Again, there was no interaction between identity and angle in this time window ($F(1,14) = 2.4$; $p = .142$).

To test whether N250r amplitudes were modulated by increasing familiarity with the face set in the course of the experiment, averaged ERP data were analysed separately for blocks 1-4 (first half of the experiment) and blocks 5-8 (second half). It has to be noted that participants were already familiar with the stimulus set, as the same faces had been used in a previous pilot study. Statistical analyses in the 250-300 ms time window after the onset of the second face showed no interaction between identity and half at posterior electrodes P7/8 ($F < 1$).

3.1.4 Discussion

Experiment 1 tested whether rapidly generated visual memory traces for unfamiliar faces would generalize across changes in view, and varying degrees of rotations. N170 amplitudes in the early time window (160-190 ms) were unaffected by identity repetitions versus changes, in line with previous findings that this component is not modulated by facial identity (Eimer, 2000c; Bentin & Deouell, 2000; but see Caharel et al., 2009). Clear N250r components were present in the subsequent 250-300 ms post-stimulus time window, demonstrating typical enlarged negativities to two faces showing the same as compared to two different individuals. Topographic scalp maps confirmed its characteristic posterior negativity that was accompanied by an anterior positivity in the same time range (see Figure 3.2, bottom panel). The presence of reliable N250r components to immediate repetitions of unfamiliar faces is consistent with previous reports (Pfütze et al., 2002; Itier & Taylor, 2004). Importantly, the present experiment employed a rapid repetition paradigm where two faces were presented within 400 ms of each other. The fact that reliable N250r components were elicited following very brief time lags between repetitions demonstrates that visual information about the identity of an unfamiliar face can be extracted very rapidly, and that newly acquired visual

memory traces are immediately available to be matched with on-line representations of individual faces. In an earlier study, N250r components to famous face repetitions were found with even shorter interstimulus intervals (17 ms; Trenner, Schweinberger, Jentzsch, & Sommer, 2004). However, this effect is likely to reflect a match between two simultaneous perceptual face representations rather than visual face memory (see Brockmole, Wang, & Irwin, 2002; Dalvit & Eimer, 2011, for the transition from percept-percept to memory-percept interactions as a function of ISI). In contrast, the ISI of 200 ms that was used in Experiment 1 was sufficiently long to prevent direct perceptual interactions between two images, and to ensure that N250r components reflect the presence of rapidly generated visual memory representations for individual faces**.**

Analyses of ERP data across all experimental blocks confirmed the presence of an N250r component. The finding that an N250r was clearly triggered by identity repetitions versus changes under conditions where two faces were always shown in two different views demonstrates that this component reflects the extraction of visual information from a face that is specific to facial identity, and does not merely reflect the encoding of more general low-level visual properties of the image. N250r components to repetitions of unfamiliar faces across view changes have been observed in one previous ERP study (see Caharel et al., 2009). However, in this study, the rotation in viewing angle between two faces always remained constant at an angle of approximately 45°. Moreover, on all trials a full-front view was preceded by a side view, a condition that is relatively easy for face identity matching, as reflected by the fact that side-front trials showed the highest accuracy and fastest RTs in the present experiment. Additionally, a long ISI of about 3 seconds was used in this study, which may have supported preparatory transformations of visual working memory representations, such as mental rotation.

The aim of Experiment 1 was to find out whether unfamiliar face recognition, as reflected by the N250r component, generalizes across large changes in view, and whether this component is modulated by the relative degree of angle rotation. To answer these questions, N250r components were measured on trials where the second of two successively presented faces was either rotated by 45° or 90° (small versus large angle). Clear N250r components were not only triggered in response to small angular rotations (i.e., side-front and side-profile trials), but also reliably emerged to large angular rotations (i.e., front-profile and profile-front trials; see Figure 3.3). Importantly, increasing the degree of angular rotation did not affect

N250r amplitudes, as components of similar size were obtained for both types of rotation. This finding is remarkable, as it suggests that unfamiliar face recognition generalizes to a substantial degree across changes in viewpoint, including large rotations in viewing angle between two sequentially presented face images. This observation strongly indicates that neural representations of individual faces are, to some extent, based on abstract visual cues that are view-independent. If the recognition of unfamiliar faces, as reflected by the N250r, was largely based on *pictorial* learning (i.e., the perception of image-based cues that are not specific to facial identity), increasing the degree of angle rotation should markedly affect this component (see Longmore et al., 2008).

When separate analyses were performed on factor half (i.e., blocks 1-4 versus blocks 5-8: first versus second half), no effects of face learning were observed. This is not surprising considering that the stimulus set did not consist of novel faces, but of faces with which participants were already familiar. Therefore, it is likely that the absence of face learning effects reflects previous perceptual exposure to the same twelve identities. Participants' overall performance on the identity-matching task showed significantly higher accuracy and faster RTs during the second experimental half as compared to the first half, but this finding is likely to reflect general training effects rather than effects specifically related to face learning.

The current findings demonstrate that unfamiliar face recognition is characterized by fast encoding and subsequent access to perceptual memory traces that reflect some kind of generalized abstract representation of an individual face. One possibly is that these abstract codes contain structural aspects of faces that are invariant across pictorial changes (Bruce & Young, 1986). Electrophysiological evidence supports this view by demonstrating a degree of image or view-independence of face-selective responses in occipito-temporal cortex, and these effects have been shown for both famous faces (Schweinberger et al., 2002a; Bindemann et al., 2008), as well as unfamiliar faces (Caharel et al., 2009; Kaufmann et al., 2008). ERP findings of a degree of invariant processing of unfamiliar face identity contrast with clear behavioural impairments in recognition memory for unfamiliar faces on tasks requiring the recognition of the same person shown from different photographs or viewpoints (e.g., Bruce, 1982; Bruce et al., 1999). This is further demonstrated by behavioural performance on the identity-matching task in the present study: Participants responded significantly faster and more accurate on trials with small rotations as compared to large angles of rotation (45° versus 90°). In other words, unlike the current ERP data, behavioural

measures indicate that face recognition was impaired on trials with a large rotation in view. This suggests that unfamiliar face recognition processes are affected by the degree of rotation between two faces and are thus not fully invariant. Moreover, same/different identity judgments were more accurate and faster on side-front trials, as compared to any of the other three view conditions, suggesting that it was easiest to match pairs of unfamiliar faces on those types of trials. This further indicates that face recognition was facilitated in the absence of a profile view (i.e., on side-front trials), whereas recognition performance was similar on trials where a profile view was present (i.e., on side-profile, front-profile, and profile-front trials), which is in line with previous findings that profile views impair face recognition memory (Hill et al., 1997).

How can the observed discrepancies between behavioural and ERP measures be explained? One possible explanation is that two different processes are involved in unfamiliar face recognition, reflecting the simultaneous activation of both pictorial and structural codes. In other words, while, ERP responses reflect the perception of invariant identity-related information about faces, behavioural measures may index the parallel activation of more general picture-based memory processes.

In summary, the present study showed that unfamiliar face recognition processes generalize to a substantial degree across rotations in viewpoint, irrespective of the relative degree of rotation. This supports the notion that visual codes for facial identity are represented in a flexible and abstract fashion, even for initially novel unfamiliar faces. Moreover, electrophysiological evidence for view-invariant identity processing following very brief time intervals between repetitions of the same face demonstrates fast encoding of and access to abstract visual codes for facial identity. However, behavioural results suggest that unfamiliar face perception may be mediated by both low-level image-based and more high-level abstract face representations. To further explore the relative roles of structural and pictorial codes in unfamiliar face recognition and the effect of face learning, Experiment 2 was conducted. This experiment directly compared N250r responses on trials where two faces were shown in either the same, or two different views.

Chapter 4. The impact of learning on face perception and visual face memory

The findings from Experiment 1 suggest that the recognition of unfamiliar faces is characterized by a degree of viewpoint-independence, which challenges the hypothesis that different neural mechanisms underlie familiar and unfamiliar face recognition. Is unfamiliar face perception and recognition based on low-level visual pictorial cues or more abstract view-independent representations of facial identity (or a combination of both)? A related question concerns the neural mechanisms of perceptual learning. Does perceptual learning alter face identity processing, as well as the dependence or independence from viewpoint? Experiment 2 addressed whether face learning changes the perceptual mechanisms by which individual faces are distinguished from one another.

4.1 Experiment 2. The emergence of view-independent recognition during face learning

4.1.1 Introduction

The previous experiment demonstrated that newly acquired face representations emerge very rapidly, and that these are characterized by a considerable degree of invariance across view. While these observations are in line with Bruce and Young's (1986), and suggest the acquisition of abstract visual representations for individual identity, several questions remain unresolved. Is unfamiliar face recognition based on structural identity-specific codes (and not on pictorial), which would be incompatible with a large body of behavioural evidence suggesting a reliance on image-specific information when identifying unfamiliar faces (see Hancock et al., 2000, for a review)? Or is the recognition of unfamiliar faces mediated by the simultaneous activation of both low-level image-based and high-level identity-specific visual information? This latter view is in line with the observed recognition impairment in Experiment 1 when increasing the degree of angular change in viewpoint between two unfamiliar faces.

An important factor mediating the dependence or independence of face recognition processes from view might relate to the visual familiarity with a face. Initially novel unfamiliar faces that have been seen a number of times become familiar. In Experiment 1, the effect of learning on the perception and recognition of individual faces could not be assessed.

Therefore, a central aim of Experiment 2 was to find out whether repeated exposure to initially novel unfamiliar faces changes the perceptual mechanisms of individual face recognition. Are view-independent representations of individual faces acquired as a result of face learning once novel faces have become more familiar? In other words, is the perception of novel unfamiliar faces based on pictorial visual cues, and are more abstract high-level representations formed during learning?

The representation of individual identity

Human face memory must accomplish the storage of more than thousands of individual faces that are encountered during a lifetime. Yet how this remarkable perceptual skill is accomplished, and how the human brain is able to extract identity-specific facial cues in spite of changes in the visual appearance of faces across different images is still largely unknown. In recent years, face research has more and more focused on the cognitive and neural processes involved in the perception of individual identity. Two different functional accounts have been put forward to explain how the same individual is recognised despite large within-person variability from one encounter to the next. According to Bruce and Young (1986), *structural* codes for facial identity need to be acquired for effective face recognition, which contain invariant cues about an individual's identity. These structural face representations are assumed to be formed over time, and mediate the recognition of highly familiar faces. The reliance on these types of structural visual cues may therefore account for our "face expertise" in recognizing familiar faces. Even though the extract nature of structural face memories and the mechanisms by which these are acquired are still largely unknown, it appears plausible to assume that the formation of these high-level identity-specific codes requires repeated exposure to the same face across many different images. This would suggest that stable visual cues of faces gradually become more independent from low-level image-specific properties (such as variations in facial expression or view). Burton et al. (2005) proposed that robust memory representations for individual faces may represent an 'average' face template of a person's face, created by merging different images of the same individual face across many different encounters.

Strong support for the existence of the abstract representation of structural aspects of faces come from infant studies. For example, Turati, Bulf, and Simion (2008) showed that newborns are able to form representations from an unfamiliar face that are to a certain

degree invariant to rotations in view. The observation that infants are able to extract abstract information for facial identity suggests that face perception is preferentially tuned to human faces, and their typical configuration, from birth. In contrast to the notion of abstract face identity processing, others (e.g., Longmore et al., 2008; Troje & Kersten, 1999) argue that different images of the same individual may instead be represented as *pictorial* (i.e., view-dependent) face memories, comprising of a discrete set of previous encountered views of the same person According to this view, individual face recognition is based on the perception of image-specific visual cues representing snapshot-like episodic face memory traces. Support for the image-dependence of visual face recognition irrespective of face familiarity comes from face learning studies. Longmore et al. (2008) tested whether learning unfamiliar faces from different views weakens the reliance on low-level properties of the encountered image indicative of view-independent identity processing, thereby facilitating face recognition across novel images. However, results showed that recognition memory of learned faces did not generalize better to novel views after participants had learned a set of unfamiliar faces shown from different viewpoints, and under different lighting conditions as compared with exposure to a single view during learning. In other words, the view-dependence of unfamiliar face recognition was unaffected by face learning.

In summary, at present there is no clear answer to how facial identity is processed and represented in human visual cortex despite large low-level image variability such as view changes. Two different accounts have been proposed to explain how humans recognize the same individual face across very different visual inputs. On the one hand, abstract structural representations for familiar faces may be acquired over time and many encounters with the same person (i.e., during learning). On the other hand, different images of the same individual face may be stored as a set of distinct pictorial representations of the specific encounter in visual face memory.

Mechanisms of face learning

Unlike unfamiliar faces, familiar faces have been encountered many times, across many different images or viewpoints. However, surprisingly little is known about the process by which novel unfamiliar faces become familiar, that is, the mechanisms underlying face learning. Learning the identity of faces could be accomplished in two ways: By extracting image-independent *structural* cues about facial identity or by forming associative links

between *pictorial* face memory traces of specific encounters with a person. These two accounts of face learning argue that learning-related neural changes occur either during early face perception (structural) or during later stages of memory consolidation (pictorial). If abstract representations of individual faces are formed during learning, one would expect to observe a shift from view-dependent to view-independent recognition as initially novel face become more familiar. In contrast, no such qualitative shift in perceptual face processes is expected, if one assumes that learning occurs during late post-perceptual stages via associative links between different images of the same individual. At present, it is unclear whether face learning involves neural changes at early perceptual or late semantic processing stages.

In most face-learning studies (e.g., Bruce, 1982; Hill et al., 1997), participants are exposed to a single view of an unfamiliar face during a study phase, and these studies have found view-dependence in the recognition of unfamiliar faces. Moreover, the many possible degrees of familiarity from a single exposure to many encounters on very different occasions make it difficult to study face learning and its underlying neural mechanisms. If structural codes are derived from novel unfamiliar faces during repeated exposure to the same individual face, increasing familiarity should result in a shift from view-dependent to view-independent face recognition. If this is correct, it should be possible to track the formation of structural identity-specific codes during learning. In contrast, if face recognition is based on image-specific visual information, irrespective of face familiarity, learning should not affect the perception of facial identity. Therefore, structural and pictorial accounts differ in the role of learning in face recognition: In the former, recognition is initially based on pictorial cues, but becomes more invariant as faces become familiar. In the latter, face recognition is based on a close match between a stored view with an encountered view, even after initially novel faces have been encountered many times.

An interesting question concerns the generalization of face recognition memory across novel views. If structural face memory traces are acquired during exposure to multiple views of the same face as compared to learning only a single view of a face, this should facilitate recognition of learned identities across novel views. Longmore et al. (2008) tested whether invariant identity-defining features of faces or general properties of the image are acquired during learning. Face recognition memory was assessed for participants who had been exposed to novel unfamiliar faces across either different views, or a single face view. If

abstract face representations are formed, identity-specific information from both views should be integrated into a single face memory of that individual. However, Longmore et al. did not find an advantage in recognizing a learned face shown in a novel view when multiple views relative to a single view had been learned. In addition, recognition accuracy was directly linked to the degree of angle change between learning and test with smaller rotations yielding higher performance (see also Hill et al., 1997). These findings suggest that recognition of newly learned faces is image-based, and that the underlying visual face memories are thus not view-independent. However, it is possible that the learning phase in Longmore et al.'s (2008) experiment was not sufficient for the formation of structural codes, which may require more encounters across more varied images to provide ample time for the extraction of viewpoint-invariant face representations. If structural codes represent a continuum depending on the number of times a face has been seen, and the number of views it has been encountered in, these codes may be imperfect during early stages of learning and only become detailed and refined after many encounters. If this is the case, face recognition should be largely view-dependent during early stages of learning, but should become increasingly more view-independent as faces become more familiar. A different explanation of Longmore et al.'s findings would be that visual memory traces of newly learned faces are based on both pictorial and structural codes, and that behavioural measures of face recognition memory therefore reflect a degree of (but no full) view-dependence.

Taken together, very little is known about the mechanisms of face learning and the neural changes that are associated with the processing of novel unfamiliar as compared to newly learned faces. Behavioural evidence suggests that face recognition processes are largely based on low-level on learning visual properties that are specific to the encountered image, even for experimentally learned faces. However, more research is needed to find out whether strictly image-based face representations may change into more flexible structural representations of individual identity as a result of face learning.

Neural basis of face learning

A review of the literature indicates that relatively little is known about the neural basis of face learning whereby initially novel faces gradually become more familiar through repeated exposure (see Chapter 1, Section 1.4.1, for a review on neural markers of face familiarity). While most neuro-imaging studies do not provide evidence for qualitative differences

between familiar and unfamiliar face processing (see Natu & O'Toole, 2011, for a review), electrophysiological research may be more sensitive to address questions about the neural processes that underlie face learning. While behavioural studies have consistently shown that familiar face recognition is invariant to a variety of image changes, whereas unfamiliar face recognition is affected by such changes (Burton et al., 1999, 2001), there is little insight the neural correlates of these differences. If qualitatively different perceptual mechanisms underlie the recognition of unfamiliar as compared to familiar faces it should be possible to track the acquisition of face familiarity over time. In an ERP study by Tanaka et al. (2006) participants were asked to recognize a previously studied target face that was presented among other non-target faces as well as the participant's own face. In the first half of the experiment, only the own face elicited an N250 component, reflecting the activation of a stored long-term face representation. In contrast, in the second half of the experiment (i.e., after the target face had become familiar), an N250 component also emerged in response to the initially novel target face. This new face representation had emerged as a result of acquired familiarity, an observation which is consistent with previous findings from repetition priming studies where N250r responses were elicited in response to both highly familiar faces (e.g., family members or celebrities; see Begleiter et al., 1995; Schweinberger et al., 1995; 2002), as well as experimentally learned faces (Itier & Taylor, 2004). Others (e.g., Kaufmann et al., 2009) have reported a similar gradual emergence of the N250 following repeated exposure to initially novel faces, even when different images of the same face were shown.

While these results demonstrate that the N250 component indexes face learning, little is known about the conditions under which new face representations are acquired. For example, all faces in the Tanaka et al. (2006) experiment were presented in a front view, and therefore the dependence or independence from viewpoint could not be assessed. If familiar and unfamiliar face recognition processes rely on different perceptual mechanisms which are defined by their respective dependence on structural versus pictorial cues, acquiring familiarity with novel faces should result in qualitative changes in the way that learned faces are represented in visual face memory. When faces are still essentially unfamiliar, face recognition should largely rely on learned information that is specific to a particular face image. In contrast, in the course of learning, a shift in identity-related face processing from generic pictorial to more abstract representations of identity-related information should be observable. As a result of many encounters with the same face across different images or

views, these representations should eventually become independent from a particular image or viewpoint.

Taken together, while behavioural evidence from face learning studies did not find facilitated recognition of learned faces across novel views, ERP evidence has identified a neural marker of face learning that emerges when initially novel unfamiliar faces become more familiar following repeated exposure to the same identities. Moreover, changes in ERP responses as a result of face learning were not only found to identical-image repetitions, but also to different images of the same face. This suggests that face memory traces of unfamiliar faces are not purely based on low-level pictorial information but on more abstract cues about individual identity.

Research aims

Experiment 2 addressed two research questions: First, are unfamiliar face recognition processes, as reflected by the N250r component, based on view-dependent pictorial or view-independent structural codes, or a combination of both? Second, is the perception and recognition of strictly unfamiliar faces view-dependent, but these processes becomes more view-independent during face learning? Participants performed a face identity matching task where two faces were presented in rapid succession on each trial. These either showed the same or two different individuals, in either the same view (view-repetition) or two different views (view-change). On view-repetition trials, face matching could solely rely on pictorial cues about the encountered image. In contrast, on view-change trials, identity matching has to rely on learning abstract information about invariant aspects of faces. If N250r amplitudes are differentially modulated by view-repetitions versus view-changes, this would suggest that the underlying representations are not fully view-dependent but based, at least partly, on view-specific pictorial codes. Moreover, if an N250r is elicited on view-change trials only in the second half of the experiment, after initially novel faces have become familiar, but is absent in the first half of the experiment, this would demonstrate the emergence of view-independent recognition during face learning.

4.1.2 Method

Participants

Twelve volunteers (six females), aged 20 to 29 years (mean age 24 years, SD = 3) were tested. Data from two further participants was excluded due to an insufficient number of

artifact-free EEG trials (less than 60% of all trials left after artifact rejection). All participants were right-handed, had normal or corrected-to-normal vision, and gave written informed consent prior to testing.

Stimuli and procedure

Face stimuli consisted of a new set of 12 unfamiliar faces (six female faces) created using FaceGen Modeller 3.4 (Singular Inversions Inc., Toronto). Faces were full-colour images, and were shown either in a front view, or in a left-facing side view at an angle of approximately 45° (see Figure 4.1, for examples). No profile views were used, as these had been shown to impair recognition memory in Experiment 1.

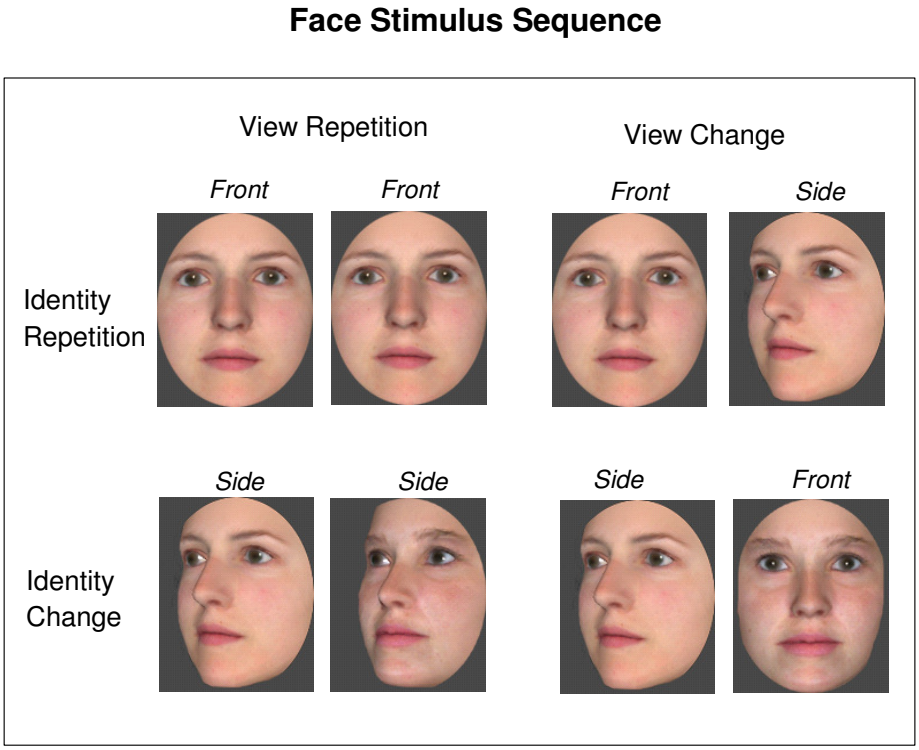


Figure 4.1 Examples of the four different face stimulus sequences. On each trial, two faces showed either the same or two different individuals (identity-repetition versus identity-change), in either the same view (front-front or side-side; view repetition) or a different view (front-side or side-front; view change). Note that the second image was always 20% larger than the first image.

All images were cropped into an oval shape using Adobe Photoshop 6.0 (Adobe Systems Inc.). In order to avoid identical stimulation of the same retinal area in trials where two physically identical faces were presented in rapid succession, the visual angle subtended by

the face presented in the first position (5.2° × 3.4°) was always smaller than the angle subtended by the second face (5.7° × 4.6°). The combination of 12 different identities, two different views, and two different sizes resulted in a total of 48 face images. All face stimuli were presented centrally on a CRT monitor against a dark grey background (4.0 cd/m^2), at a viewing distance of 100 cm, using E-Prime software (Psychology Software Tools, Pittsburgh, PA). Their average luminance was 20.1 cd/m^2

Temporal parameters of stimulus presentation were identical to those used in Experiment 1. Two faces were presented in rapid succession for 200 ms each, separated by a 200 ms interstimulus interval (ISI). The intertrial interval was 1500 ms. Each face pair was equally likely to show the same or two different individuals, and the same or two different views. Face view (front or side) was fully counterbalanced across face pairs. For the purpose of analysis, the factor view had two levels: view-repetition (collapsed across front-front and side-side trials) and view-change (collapsed across front-side and side-front trials). Eight experimental blocks of 80 trials were run, with self-paced breaks, and a longer break after block 4. Forty trials per block (10 for each of the four combinations of view: front-front, side-side, front-side, or side-front) included faces of two different individuals. In the other 40 trials, the same individual was shown.

The view of the second face of each pair (front or side view) remained constant within each block, and was changed across successive blocks. Six participants started with a block where the second face was always presented in a front view, and the other six started with a side view block. Participants performed an identity-matching task. They were instructed to respond with a left-hand button press on trials where a face pair showed the same individual (regardless of whether their view was the same or different), and with a right-hand button press when two different individuals were shown. The experiment lasted about 25 minutes, and was preceded by two training blocks.

EEG recording and data analysis

These were identical to Experiment 1. Following artifact rejection, EEG waveforms were averaged separately for each combination of identity (identity-repetition versus identity-change) and view (view-repetition versus view-change). Mean amplitude values were computed at posterior electrodes P7/8 for the N170 time interval (160-190 ms after the onset of the second face) and for the N250r time interval (210-260 ms after the onset of the second

face). Additional analyses were conducted for the subsequent 260-310 ms post-stimulus time interval. Repeated-measures analyses of variance (ANOVAs) were performed for factors identity (identity-repetition versus identity-change), view (view-repetition versus view-change), and hemisphere (left versus right: P7 versus P8). Analogous analyses were also conducted at frontal electrode Fz. To assess the effect of face learning, N250r components were analysed separately for the first half (blocks 1-4) and the second half (blocks 5-8) of the experiment. These analyses included the additional factor half (first half versus second half).

4.1.3 Results

Behaviour

Participants correctly matched facial identities on 92% of all trials. Accuracy was higher for same identity as compared to different identity judgments (95% versus 90%; $F(1,11) = 6.4$; $p < .03$), and for view-repetition as compared to view-change trials (95% versus 90%; $F(1,11) = 20.6$; $p < .01$). There was no interaction between identity and view for accuracy ($F < 1$). Accuracy did not differ between the first half (blocks 1-4) and the second half (blocks 5-8) of the experiment, and there was no interaction between identity and half, or three-way interaction (identity x view x half: all $F < 1$).

Mean correct RT was 526 ms. Responses were faster on trials where both identity and view were repeated (462 ms) than on trials with a view change, an identity change, or a change of both attributes (531 ms, 552 ms, and 563 ms, respectively). This was reflected by main effects of identity ($F(1,11) = 24.3$; $p < .001$), view ($F(1,11) = 58.5$; $p < .001$), and a significant interaction between both factors ($F(1,11) = 14.3$; $p < .01$). RTs were significantly faster in the second half of the experiment than in the first half (512 ms versus 543 ms; $F(1,11) = 5.4$; $p < .05$). An additional analyses for successive pairs of blocks revealed that RTs were faster in blocks 3 and 4 (531 ms) relative to blocks 1 and 2 (554 ms), and faster in blocks 5 and 6 (508 ms) relative to blocks 3 and 4 (both $p < .05$). A three-way interaction between identity, view, and half approached significance for RTs ($F(1,11) = 4.2$; $p < .07$). On view-change trials, RTs for identity-repetition judgments were significantly faster than RTs for identity-change judgments in the second half of the experiment (513 ms versus 553 ms; $F(1,11) = 2.3$; $p < .05$), but not in the first half (550 ms versus 574 ms; $F(1,11) = 1.2$; $p > .24$).

Separate analyses were also conducted for factor view condition (e.g., front-front, side-side, front-side, or side-front). These showed a main effect of view condition ($F(3,33) = 15$; $p <$

.001) , but no interaction between identity and view condition ($F < 1$) for accuracy. Follow-up analyses demonstrated that accuracy on front-front and side-side trials (95% and 94%; i.e., view-repetition trials) differed significantly from accuracy obtained on side-front and front-side trials (both 90%; i.e., view-change trials). For RT, there was a main effect of view condition ($F(3,33) = 15$; $p < .001$), reflecting significantly faster RTs on front-front and side-side trials (507 ms each) than on side-front and front-side trials (536 ms and 559 ms). A significant interaction between identity and view condition ($F(3,33) = 12.5$; $p < .01$) was followed up with paired t-tests. These demonstrated significant main effects of identity for front-front and side-side trials (i.e., view-repetition; $t(11) = 6.1$ and 7.4; both $p < .01$), as well as for as well as for side-front trials ($t(11) = 2.7$; $p < .03$). No main effect of identity was present for front-side trials ($t < 1.2$).

ERP markers of visual face memory: All blocks

Figure 4.2 (top panel) shows ERP grand averages elicited on identity-repetition and identity-change trials at posterior electrode pair P7 and P8 in the 400 ms interval after the onset of the second face in a pair. ERPs are shown separately for view-repetitions and view-changes. A reliable N250r was elicited for both view repetitions and view changes and topographic scalp maps of N250r difference waves showed typical posterior negativities to repetition of the same as compared to two different identities (see Figure 4.2, bottom panel).

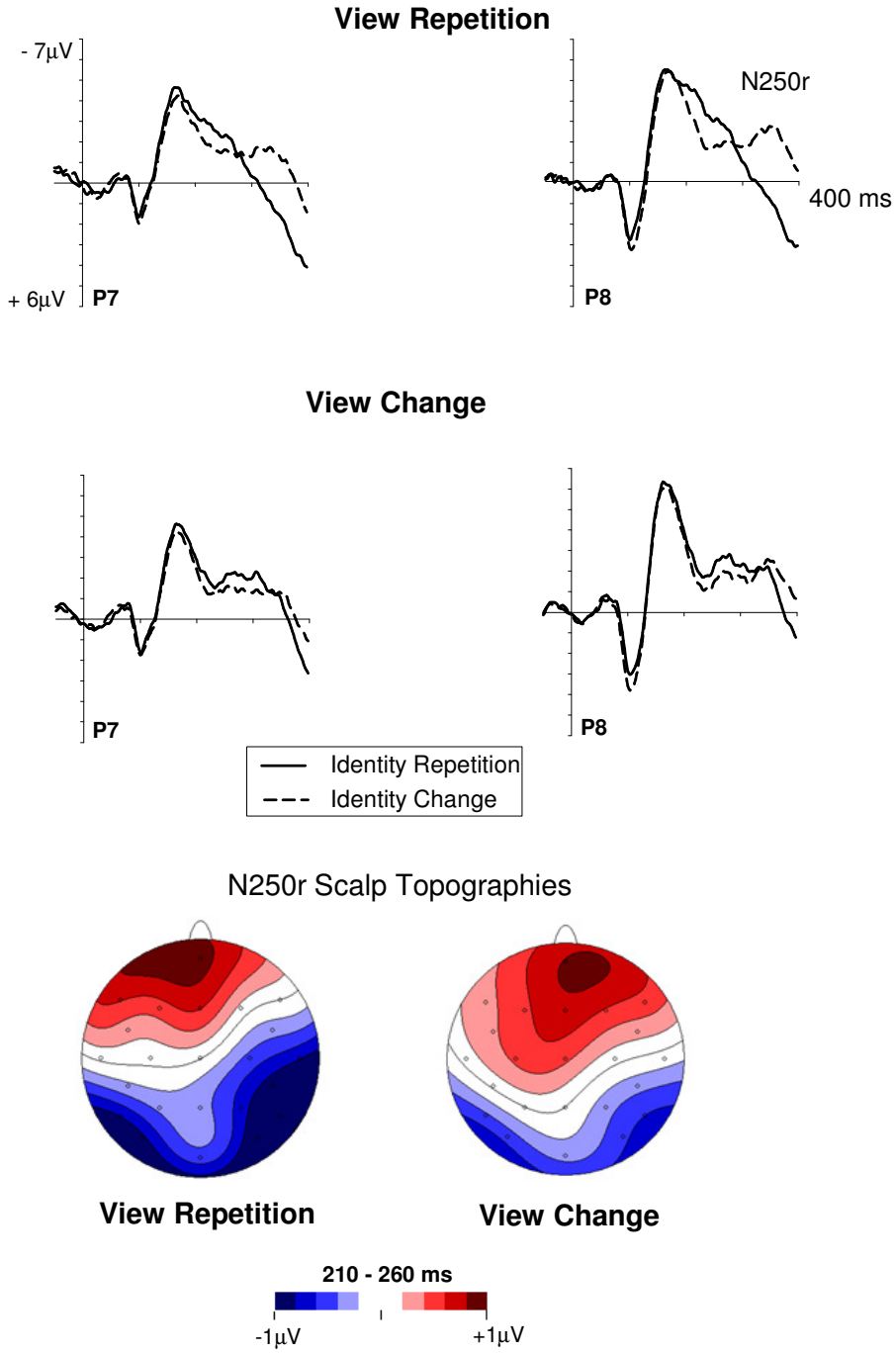


Figure 4.2 Top panel: Grand-averaged ERPs elicited at lateral posterior electrodes P7/8 in the 400 ms interval after the onset of the second stimulus in a face pair, for identity-repetition trials (solid lines) and identity-change trials (dashed lines). ERPs are shown separately for view-repetition and view-change trials. Bottom panel: Topographic maps of N250r difference waves (identity-change - identity-repetition) in the 210-260 ms post-stimulus time window, shown separately for view-repetition and view-change trials. Enhanced negativities are shown in blue, enhanced positivities in red.

There was no significant main effect of identity on N170 amplitudes at P7/8 in the 160-190 ms post-stimulus time window ($F(1,11) = 3.2$; $p < .10$), confirming that the N170 was unaffected by changes versus repetitions of identity. A main effect of identity was present in the subsequent N250r time window (210-260 ms; $F(1,11) = 12.1$; $p < .01$), demonstrating clear N250r components to same identity repetitions, and this was the case for both view-repetitions and view-change trials. An identity x hemisphere interaction ($F(1,11) = 7.0$; $p < .03$) indicated that the N250r component tended to be larger over the right hemisphere. However, follow-up analyses confirmed the presence of a reliable N250r both at right-hemisphere electrode P8 ($F(1,11) = 19.5$; $p < .01$) and left-hemisphere electrode P7 ($F(1,11) = 6.1$; $p < .04$). Even though the N250r was numerically larger on view-repetition trials as compared to view-change trials (see Figure 4.2, top panel), the interaction between identity and view only approached significance ($F(1,11) = 3.9$; $p < .08$). Separate analyses were conducted for each level of the factor view, and these demonstrated that reliable N250r components were elicited on view-repetition trials ($F(1,11) = 10.3$; $p < .01$) as well as on view-change trials ($F(1,11) = 8.7$; $p < .02$). Separate analyses performed for the factor view condition showed that N250r amplitudes were not significantly modulated by any of the four view conditions (identity x view condition: $F(1,11) = 2.5$; $p < .09$).

Analogous analyses were performed at frontal electrode Fz in the 210-260 ms time interval, where a main effect of identity approached significance ($F(1,11) = 4.6$; $p < .06$). Visual inspection of the grand averages indicated a later onset of this frontal positivity during the subsequent 260-310 ms time window, which was confirmed by statistical analyses ($F(1,11) = 22.2$; $p < .01$). There was no interaction between identity and view in this later time window ($F(1,11) = 1.3$; $p > .27$).

Effects of face learning (first versus second half)

To demonstrate the effects of face learning on the N250r component, ERPs measured in blocks 1-4 (first half of the experiment) and in blocks 5-8 (second half) were averaged separately. Figure 4.3 shows ERPs triggered at lateral posterior electrodes P7 and P8 on identity-repetition and identity-change trials, separately for view-repetition (top panels) and view-change trials (bottom panels), and for first and second half of the experiment.

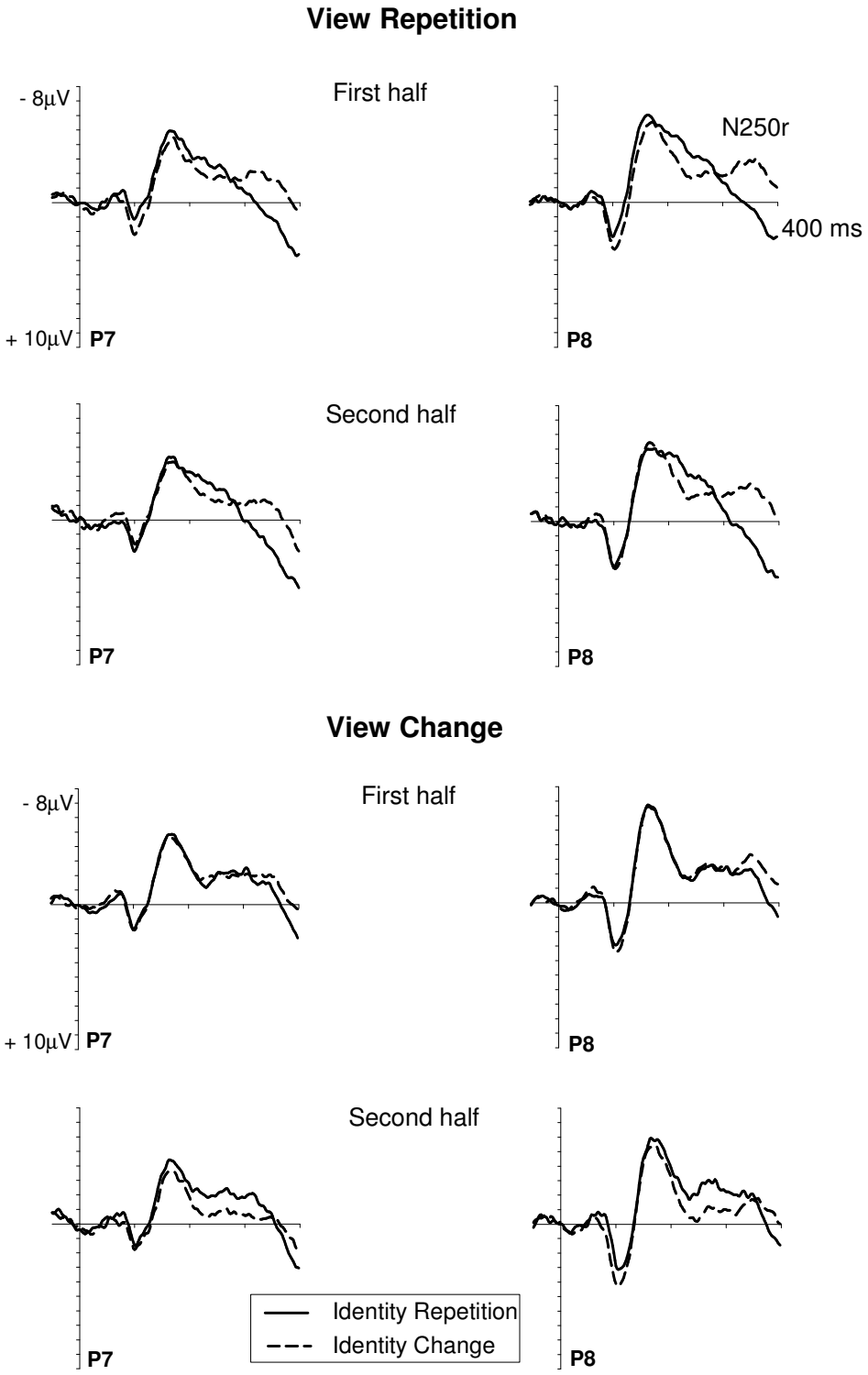


Figure 4.3 Grand-averaged ERPs measured at lateral posterior electrodes P7 and P8 in the 400 ms interval after the onset of the second stimulus in a face pair, for identity-repetitions (solid lines) and identity-changes (dashed lines), separately for view-repetition trials (top panels) and view-change trials (bottom panels). ERPs are shown separately for the first half (blocks 1-4) and the second half (blocks 5-8).

When both faces in each pair showed the same view, N250r components were already present in the first half of the experiment, and these were very similar to the N250r observed in the second half (Figure 4.3, top panels). A very different pattern was found for view-change trials: Here, N250r components were absent during the first half of the experiment, and only emerged during the last four blocks (Figure 4.3, bottom panels). These observations were confirmed by statistical analyses of ERP mean amplitudes measured in the N250r time window at P7 and P8. A main effect of identity ($F(1,11) = 13.2$; $p < .005$) was accompanied by an interaction between identity and half ($F(1,11) = 6.2$; $p < .04$), and by a three-way interaction (identity x view x half: $F(1,11) = 6.6$; $p < .03$). This was further assessed in separate analyses for view-repetition and view-change trials. For view-repetition trials, there was a main effect of identity ($F(1,11) = 10.5$; $p < .01$), but no interaction between identity and half ($F < 1$), confirming that the N250r was essentially unchanged between the first and second half of the experiment. Reliable N250r components were indeed present not only in blocks 5-8 ($F(1,11) = 11.4$; $p < .01$), but already in blocks 1-4 ($F(1,11) = 8.2$; $p < .02$). A very different pattern was observed for view-change trials. Here, a main effect of identity ($F(1,11) = 9.5$; $p < .02$) was accompanied by a significant interaction between identity and half ($F(1,11) = 7.6$; $p < .02$). Follow-up analyses demonstrated that the N250r was absent on view-change trials in the first half of the experiment ($F < 1$), but reliably present during the second half ($F(1,11) = 14.0$; $p < .005$). The same pattern was also evident when analyses were conducted separately for each experimental half. An interaction between identity and view for the first four blocks ($F(1,11) = 9.6$; $p < .02$) reflected the presence of the N250r on view-repetition trials, and its absence on view-change trials. In blocks 5-8, no such interaction was obtained ($F < 1$), demonstrating that the N250r was now elicited in a view-independent fashion.

As can be seen in Figure 4.3 (bottom panels), the N250r was more sustained on view-change trials in the second half of the experiment than on view-repetition trials in either half. This difference was assessed in analyses of ERP mean amplitudes measured at P7/8 in the 260-310 ms time window. For view-repetition trials, there was no main effect of identity and no identity x half interaction (both $F < 1$), demonstrating that the N250r had already disappeared during this time window. In contrast, there was a significant identity x half interaction for view-change trials ($F(1,11) = 5.7$; $p < .05$). Follow-up analyses confirmed that the N250r remained present during this 260-310 ms interval in blocks 5-8 ($F(1,11) = 6.6$; $p < .05$), where it was absent in blocks 1-4 ($F < 1$). To pinpoint the exact block in which N250r

components emerged when view changed between repetitions, separate analyses were conducted for blocks 4 and 5 on view-change trials only. Statistical analyses revealed the presence of clear N250r components in block 5 ($F(1,11) = 6.5$; $p < .03$; see Figure 4.4), whereas no main effect of identity was present in block 4 ($F < 1$).

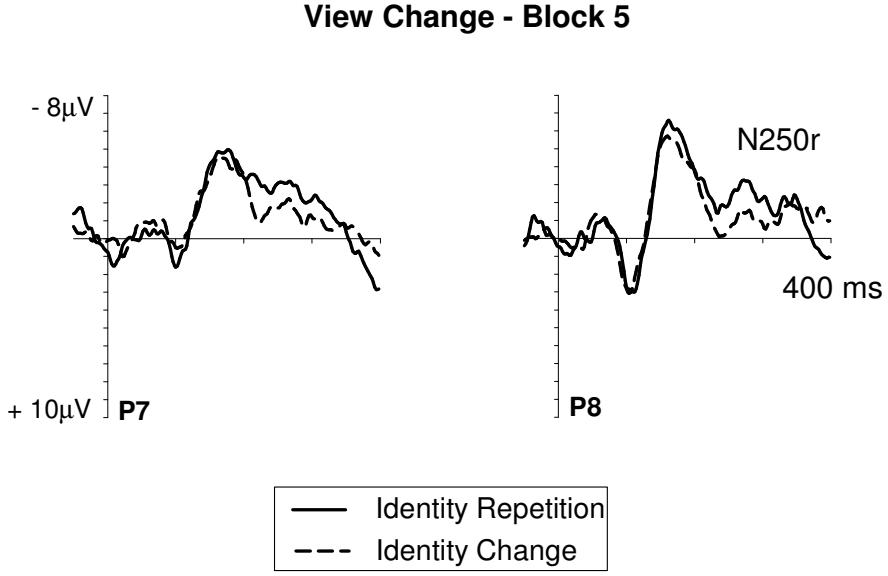


Figure 4.4 Grand-averaged ERPs elicited at posterior electrode pair P7/8 on view-change trials in block 5 of the experiment for identity-repetitions (solid lines) and identity-changes (dashed lines).

4.1.4 Discussion

Experiment 2 investigated whether unfamiliar face recognition is based on the extraction of low-level *pictorial* codes or more abstract *structural* information about facial identity (or a combination of both). In addition, it was tested whether experimentally acquired familiarity with faces would result in a change in the underlying perceptual face matching processes, that is, in the way that individual faces are processed and represented in visual face memory. On each trial, two images depicting either the same or two different individuals were presented in rapid succession, and these faces showed either the same or two different views. Participants performed same/different identity judgments on each trial, regardless of the view in which faces were shown. In line with previous findings, N170 amplitudes were not affected by identity repetition versus changes (e.g., Bentin & Deouell, 2000; Eimer, 2000c). In

contrast, characteristic posterior N250r components were triggered by identity repetitions versus changes, confirming fast encoding and subsequent access to newly acquired perceptual face representations within 300 ms after the repeated presentation of the same individual face.

Analyses of ERP data across all experimental blocks showed that a clear N250r was elicited on both view-repetition trials and view-change trials, reflecting its independence from viewpoint (see Experiment 1). Although N250r amplitudes were numerically reduced on view-change relative to view-repetition trials, the interaction between identity and view failed to reach statistical significance, suggesting that N250r components of similar size were triggered on both types of trials. This is in line with previous demonstrations of view-independence of the N250r in response to famous faces (Bindemann et al., 2008), suggesting that similar neural processes underlie the recognition of both highly familiar faces (e.g., celebrities) and experimentally learned faces. These observations appear to contradict the hypothesis that the recognition of unfamiliar faces is fundamentally different from the recognition of familiar faces. However, as the twelve facial identities used in the present study were repeated a number of times throughout the experiment in two different views (i.e., roughly 25 repetitions of each face in each view), this should gradually have increased familiarity with the face set.

When separate analyses were performed for the first and second experimental half, it became apparent that face learning had a prominent effect on the view-dependence of individual face recognition. In the first half of the experiment (blocks 1-4), a clear N250r was elicited when identical face images were repeated and identity matching could have been based on image learning. In contrast, on trials with a view change, N250r components were absent during the first experimental half (see Figure 4.3, bottom panel), demonstrating that those initial face matching processes recruited for novel faces were based solely on view-dependent pictorial codes. However, if structural representations for individual faces are acquired after repeated exposure, their activation by another presentation of the same face should elicit an N250r. That is exactly what was found in the second half of the experiment: Clear N250r components were triggered both on trials where the same view was repeated as well as on trials with a change in view. This is in line with the prediction that on view-change trials, identity processing is based on abstract structural codes, which are acquired after repeated encounters of the same face across different viewpoints. In other words, after

repeated exposure, visual cues about a person's identity had been learned, resulting in the presence of the N250r and its view-independence in the second experimental half. This observation is remarkable, as it suggests that acquired familiarity with initially novel faces through repeated exposure triggers a qualitative change in the underlying face recognition processes. During the first few encounters with a novel face, only low-level pictorial features are encoded. Learning invariant aspects of individual faces through repeated exposure then results in the formation of more abstract face representations that show a considerable invariance across image transformations such as view changes.

How many encounters with an individual face are required to produce the acquisition of view-independent face representations? This is likely to depend on the distinctiveness of individual faces, where highly similar faces require more repetitions across different images. This would explain why in the present study where computer-generated faces were used (which are generally quite similar to each other, see Figure 4.1), a face had to be seen roughly 25 times in each of the two views for an invariant face memory trace to be generated. To determine more precisely the point in time when N250r components emerged on view-change trials, separate analyses were conducted on averaged ERP waveforms on the basis of EEG data obtained for experimental blocks 4 and 5 only. As shown in Figure 4.4, the N250r was reliably present over both hemispheres in block 5, whereas there was no differential ERP modulation by identity repetitions versus changes in Block 4. The rapid emergence of the N250r in block 5 might point to an important role of face memory consolidation processes in the generation of view-independent codes, as participants were encouraged to take a short break halfway through the experiment.

There is general consent that our ability to recognize individual faces despite changes in the visual appearance has to rely on some kind of abstract neural representation of facial identity. According to Bruce and Young (1986), this involves the formation of invariant *structural* codes, which qualitatively alter early perceptual face processing stages where identity-relevant visual information is extracted from a face. However, an alternative explanation is that face perception and recognition relies on image learning, that is, on the encoding of multiple face images in visual memory (Longmore et al., 2008). According to this account, face recognition is solely based on pictorial codes for both unfamiliar as well as familiar faces. Face learning then results in the generation of associative links in memory between different episodic representations of the same individual face. Invariant recognition

of familiar faces across novel views is possible as long as one of the many stored images of that particular person represents a close match between an encountered image with a stored image. According to this view, increasing familiarity with a face does not affect early perceptual face processes, but later mechanisms in visual face memory. Based on findings from Experiment 2, it is not possible to dissociate whether face learning fundamentally affects early perceptual or instead subsequent face memory processes. As the N250r component reflects a successful match between face perception and face memory, it could in principle reflect neural changes at either stage.

One important question remains: If abstract face representations only emerged in the second half of the experiment, how did participants perform the identity-matching task on view-change trials in the first half? One possible explanation is that in this case identity judgments were based primarily on more generic low-level visual cues, such as the overall shape or distinctive surface features of individual faces (e.g., colour and pigmentation patterns), that is, on learning specific properties about the image that remained identical across view changes. The fact that accuracy was already close to ceiling in the first experimental half indicates that the identity-matching task was relatively easy, and certainly less challenging than previous behavioural tests of unfamiliar face recognition, such as tasks where a target face has to be identified among a set of candidate face photographs (Bruce et al., 1999, 2001). However, RTs were significantly faster for identity repetitions as compared to changes on view-change trials in the second but not in the first half, which points to a facilitation of face recognition by abstract identity-specific codes once faces had become visually familiar.

The current findings also have implications for our understanding of the face recognition processes that give rise to the N250r component: The absence of an N250r on view-change trials when only a generic feature-matching strategy could be applied in blocks 1-4 implies that this component is not generated when a visual match is entirely based on local visual features, but is more specifically associated with matching processes that compare global-configural information about facial identity. In addition, the present data indicate that the availability of both pictorial and structural codes gives rise to the N250r, as similar components were triggered by both view-repetition trials in the first half and view-change trials in the second half of the experiment (see Figure 4.3). This observation is in line with a previous study (Schweinberger et al., 2002a), which found that similar N250r components are

elicited in response to repetitions of identical as well as two different images of the same face, even though larger amplitudes were obtained when identical images were shown. Despite the similarity of N250r amplitudes on view-change and view-repetition trials, closer inspection of the grand averages revealed that this component was more short-lived for identical view repetitions in both first and second half. In contrast, on view-change trials an N250r was reliably present during the 260-310 ms post-stimulus time interval where it had already disappeared on view-repetition trials. This sustained negativity may be interpreted as reflecting the difficulty to access structural relative to pictorial codes.

To conclude, the present results demonstrate the impact of face learning on the view-dependence of unfamiliar face recognition. A qualitative change in identity-related perceptual face processing from view-dependence to independence was observed once faces had become visually familiar through repeated exposure, presumably reflecting the acquisition of abstract high level codes for facial identity. In line with previous suggestions (e.g., Hancock et al., 2000), these findings show that unfamiliar face recognition initially operates on the basis of view-dependent pictorial codes. During face learning, view-invariant abstract representations of individual faces are then acquired which facilitate face recognition processes.

4.1.5 General Discussion. Experiments 1 and 2

How does the brain process facial identity across different images, for example when a face is shown from different viewpoints? One explanation is by means of abstract structural codes that only contain those features of a face that define its identity (e.g., Bruce & Young, 1986). Alternatively, face recognition may be based on a set of stored episodic representations of an individual face depicted in different views (e.g., Longmore et al., 2008). Experiments 1 and 2 of the present thesis investigated how individual unfamiliar faces are processed and recognized across changes in viewpoint. N250r ERP components were measured, representing neural markers of a successful match between an on-line face and a stored perceptual face representation. If the N250r is elicited in response to rapid repetitions of the same individual face across view changes, this would indicate the view-independence of unfamiliar face recognition. This is exactly what was found in Experiment 1, where two faces were presented within 400 ms of each other and face view always changed between repetitions: Clear N250r components were present across view changes, and importantly the

size of this component was not modulated by the relative degree of angle rotation, suggesting that unfamiliar face perception is viewpoint-invariant.

However, an alternative explanation is that face recognition relies on the simultaneous processing of both high-level structural and low-level pictorial codes, which would explain the observation of impaired recognition memory for large relative to small rotations in viewing angle in Experiment 1. To investigate the effect of face learning on identity-sensitive perceptual face processes, Experiment 2 was designed, which directly compared N250r amplitudes during view-repetitions as compared to view-changes, separately for first and second experimental half. Overall, analyses showed that an N250r component of similar size was triggered on both view-repetition and view-change trials. Importantly, results showed that repeated exposure to individual faces during the experiment changed the nature of the underlying perceptual face mechanisms. On view-change trials requiring identity learning, an N250r component was absent in the first experimental half, but clearly emerged during the second half of the experiment, reflecting the acquisition of view-independent codes of facial identity during face learning.

What implications do the current findings have for our understanding of perceptual face recognition processes that give rise to the N250r component? First, the present data highlight the ability of the human face recognition system to rapidly extract identity-related information about individual faces. Second, repeated exposure to individual faces results in the learning of identity-specific visual information about faces, as reflected by the emergence of N250r components on view-change trials in the second half of Experiment 2 when unfamiliar faces had become more familiar. These findings suggest that face-identity matching of learned faces is based on more abstract identity learning as compared to mere image learning. Moreover, results highlight an important distinction between familiar and unfamiliar face recognition: Novel unfamiliar faces that have been encountered a number of times and in different views become visually familiar, displaying those image-invariant properties that have so far mainly been associated with the recognition of highly familiar faces. This is in line with the view that qualitative differences underlie the recognition of familiar and unfamiliar faces, but only as long as unfamiliar faces are essentially novel and have only been seen on a very few number of occasions. Recognition of such novel faces was indeed solely based on low-level pictorial cues. However, qualitative differences in face

recognition mechanisms emerged during the early identity-sensitive perception of individual faces and, most importantly, differentiated essentially novel from visually familiar faces.

It has to be noted that even though participants acquired a degree of perceptual familiarity with the stimulus set in both experiments, representations of experimentally learned faces should still differ markedly from those of highly familiar faces (e.g., celebrities or family members). Structural face representations for visually familiar faces should be less robust and generalized, as they are limited by the conditions of initial exposure – the limited number of encounters along with the limited amount of variation in changeable aspects of faces, such as exposure to only two different views. In contrast, highly familiar faces have been seen many times, and in many different views, resulting in the acquisition of stable and view-invariant representations. Nevertheless, in the course of Experiment 2, initially novel faces became sufficiently familiar to demonstrate view-independent face recognition. Do these results imply that similar face recognition processes mediate the perception of visually familiar and highly familiar faces? The observed qualitative change from view-dependent to view-independent recognition suggests that the same perceptual mechanisms that are involved in identity-related processing of highly familiar faces are rapidly engaged once novel faces have become familiar. This would suggest that once view-invariant codes of facial identity have been formed (e.g., as reflected by the observed qualitative change in perceptual face recognition), increasing encounters with the same individual face result in stronger neural responses as a function of increasing familiarity, but do not fundamentally alter the underlying neural representations. According to this view, the important shift in face recognition from image learning towards face identity learning occurs relatively early during face learning.

How does the fast acquisition of invariant unfamiliar face recognition fit in with the observed difficulty in matching unfamiliar faces from different photographs? This discrepancy may partly be due to differences in the difficulty of face-matching tasks. In Experiments 1 and 2, where different views of the same face shared some pictorial features, face matching proved to be relatively simple, in marked contrast to previous paradigms, where a target face had to be identified among a line-up of faces (Bruce et al., 1999; 2001). The similarity of the two different views and the frequent exposure to the same facial identity in these two experiments may have aided the formation of structural face representations. Therefore, sufficient training across relatively controlled image variations may be crucial to allow the

formation of view-invariant visual face memories. Another important factor for the emergence of view-independent face recognition might relate to the rapid repetition paradigm employed in Experiments 1 and 2 where two faces were presented within 400 ms from each other. As little is known about the longevity of newly acquired perceptual face representations (but see Chapter 7 of the present thesis), visual face memory traces may decay rapidly and may only be temporarily available in visual working memory (WM).

In summary, findings from Experiments 1 and 2 provide new insights into the perceptual mechanisms that underlie unfamiliar face recognition processes, and the impact of face learning on the view-dependence of unfamiliar face recognition. Results demonstrate that the recognition of essentially novel faces is based on image-based view-dependent representations. During face learning when unfamiliar faces become more familiar through repeated exposure, these representations become view-independent. This qualitative change from view-dependent to view-independent recognition as a result of learning is likely to reflect the acquisition of structural identity-specific codes, but could also reflect the formation of associative links between sets of view-specific pictorial representations of individual faces. The observed view-independence of individual face processing is assumed to contribute to the long-term memory representations of familiar faces.

Chapter 5. Attention and automaticity in individual face recognition

Human faces attract attention, which facilitates both early stages of face perception and subsequent recognition of a familiar individual (e.g., Haxby et al., 1994; Wojciulik, Kanwisher, & Driver, 1998). Among the wealth of information that a face provides, some facial aspects may be processed with little or no attention, that is, in an "automatic" fashion. The following three experiments (Experiments 3-5) addressed how attention is involved in recognizing facial identity. Is identity-related information extracted from a face in an obligatory way, even when there is no need to encode its identity? In other words, do face recognition processes operate independent of selective attention and/or current task demands? Or is selective attention required to encode subtle individual differences that distinguish one face from another?

Given the limited processing capacity of the human visual system, not all information can be processed at one time. Instead, some visual objects or features are selectively attended to while others are ignored (e.g., Desimone & Duncan, 1995). When processing a human face, only some of the many available cues receive attention based on current goals (i.e., searching for a familiar face in a crowd or monitoring facial expressions during social interactions). The common failure to recognize a known face in an unusual context highlights the fact that face recognition is facilitated when it is intended and when processing is directed to the unique visual aspects of an individual's face that define its identity. However, interactions between face perception and attention are still poorly understood. What type of information is extracted from a face irrespective of attentional focus (i.e., task demands) and thus in an obligatory way? At present, relatively little research has provided insights into the functional role of selective attention for individual face recognition. Experiment 3 tested whether unfamiliar face recognition processes are activated in an automatic fashion in a task where participants match the view of two sequentially presented faces, while their identity is task-irrelevant.

5.1 Experiment 3. Face recognition on implicit identity-unrelated tasks

5.1.1 Introduction

A great part of the visual world around us is processed automatically, that is, rapid, effortlessly and with little or no attention or cognitive control. Neural processes, which are characterized by a degree of automaticity, are difficult to alter or inhibit and thus contrast

with intentional processes which are effortful, controlled and guided by selective attention (Moors & De Houwer, 2006). While the term automaticity is often interpreted as fully involuntary processing, it appears likely that different degrees exist between strictly optional and strictly obligatory processing. The automatic-controlled dimension represents a continuum rather than a dichotomous distinction where different aspects of automaticity are closely intertwined, such as intentionality (i.e., task goals), attention (i.e., selectivity) and conscious awareness.

Face processing is characterized by a sequence of distinct processing stages where the initial detection of a face is followed by the identification of a known person. An interesting question concerns whether distinct face processing operate in an optional (i.e., task-dependent) or obligatory fashion. While Chapters 1 and 2 focused on the perception of unique facial identity, a second focus of the present thesis was to address the role of selective attention for the perception and representation of identity-specific visual information. The fact that both the detection and recognition of faces is facilitated when processing is intentional suggests a strong influence of attention on the underlying face processes (e.g., Haxby et al., 1994). Moreover, given the speed and accuracy with which humans perceive faces, it has been suggested that the processing of some facial aspects may be automatic and therefore independent from attention (see Palermo & Rhodes, 2007, for a review). The importance of attention for face recognition is also incorporated in Bruce and Young's (1986) face recognition architecture. In this model, a module called 'directed visual processing' guides our attention to goal-relevant facial features that receive in-depth processing (e.g., identifying a known face) at the expense of other visual aspects (e.g., monitoring facial expression). In other words, Bruce & Young argue that face processing is already strongly task-set dependent during the initial structural encoding stage where an individual's unique facial features are extracted. Moreover, the focus of visual processing can be flexibly directed to the analysis of different types of facial information (e.g., visual-perceptual or semantic) in line with a person's cognitive goals. Bruce and Young (1986) further propose a clear distinction between face recognition processes that are selective and strategic on the one hand and those that are passive and involuntary on the other hand. The relative degree to which face perception relies on optional as compared to obligatory processes may be related to the familiarity with a particular face. Recognizing an unfamiliar face may require attention to its identity while familiar face recognition may operate primarily in an automatic fashion.

Detecting a human face is a remarkably fast and effortless process, which suggests that it is characterized by a degree of automaticity. A large body of research from different experimental paradigms has provided converging evidence for a special status of faces in attracting and capturing visual attention. Infants preferentially attend to faces (Johnson, Dziurawiec, Ellis, & Morton, 1991), and strong support for a processing advantage for faces comes from neglect patients who detect line-drawn faces in the impaired hemifield more often than scrambled faces or other objects (Vuilleumier, 2000). These findings suggest that, unlike other objects, ignored or unattended faces attract visual attention and are particularly hard, if not at times impossible, to ignore. This may be partly attributable to the fact that faces are emotionally highly salient visual stimuli (Compton et al., 2003).

Automaticity in individual face recognition

While initial face-nonface categorization appears to involve a degree of mandatory processing, little consensus has been reached about whether or not attention is required for later stages of face processing. In other words, does automatic face processing go beyond the simple detection of faces and does it include certain aspects of identity and semantic processing? It has been suggested that in contrast to face detection, recognizing faces based on subtle individual differences may require selective attention (Palermo & Rhodes, 2002). But is identity-specific face processing fully optional and thus strictly task-dependent? At present, relatively little research has investigated under which conditions individual face recognition requires intentional processing, and when it occurs instantaneously and regardless of one's own goals. Evidence from early repetition priming studies suggests that the recognition of familiar faces is not strictly task-dependent, but occurs in an obligatory fashion (Ellis, Young, & Flude, 1990). Repetition priming refers to the phenomenon that a familiar stimulus that has previously been processed will be recognized faster and more accurately when encountered for the second time. Participants in Ellis et al.'s (1990) study performed two tasks: In Task 1, participants performed sex or expression judgments on famous faces, followed by explicit familiarity judgments (Task 2) on the same set of faces as used in Task 1 or on novel faces. Priming effects were observed for previously encountered famous faces relative to novel faces during familiarity judgments in Task 2, even though sex or expression and not identity had been the to-be-matched facial feature during the initial

exposure phase (in Task 1). Based on these findings, Ellis et al. concluded that the identity of familiar faces is impossible to ignore and therefore processed in an automatic fashion.

Behavioural priming effects for task-irrelevant faces have also been observed for unfamiliar stimuli. Khurana, Smith, and Baker (2000) showed that presenting to-be-ignored distractor faces impaired performance on a subsequent face-identity matching task where the same faces that previously served as distractors were now presented as target faces. The finding of negative priming effects when initial distractor faces had become target faces suggests that their identity was incidentally encoded on the first encounter even though participants were instructed to ignore them. Thus, some information about the identity of unattended faces was processed irrespective of task demands and following very brief exposure with entirely novel faces. Moreover, mandatory face recognition did occur even under conditions where it was not beneficial. Taken together, evidence from behavioural priming studies demonstrates that some information about facial identity is processed in an obligatory fashion, regardless of whether or not observers are familiar with the face stimuli. But what is the nature of perceptual memory representations for individual faces that are incidentally encoded? It appears plausible that the absence of visual attention influences the depth with which visual stimuli are processed. In other words, a richer and more detailed visual memory trace is likely to be formed for intentional processing as compared with shallow encoding of unattended stimuli. Boutet, Gentes-Hawn, and Chaudhuri (2002) examined the impact of visual attention on holistic face processing, as measured by the composite face effect. Before seeing the face composites, participants viewed a series of stimuli of overlapping semi-transparent face and house images. During this learning phase, participants were instructed to trace the outline of either the face (attend face) or the house (attend house). This was followed by a recognition test, where the previously viewed face images were presented as either aligned or misaligned face composites. Participants reported whether or not they had seen the top half of each stimulus during learning. Directing attention away from the face was found to result in lower accuracy on the recognition test. Furthermore, misaligned faces were recognized better than aligned faces and this composite effect was found for both *attended* as well as *unattended* faces. This suggests that attention enhances the degree to which faces are encoded in memory, but not the way in which they are processed (i.e., in an holistic fashion).

Another defining feature of automaticity is the presence of brain responses that indicate familiarity with a visual stimulus despite a complete lack of conscious recognition. Some processing does not reach consciousness, and such processing can be thought of as automatic. The question arises whether the identity of a face is processed even when people are unaware of this information. Strong cases for the existence of non-conscious processing of facial identity are findings of covert neural markers of familiarity in individuals with prosopagnosia (e.g., Eimer et al., 2012; see Chapter 8 for ERP markers of implicit face identity processing in DP). Even though face recognition ability is severely impaired in prosopagnosia, in some cases neural responses nevertheless systematically distinguish between non-recognized familiar and unfamiliar faces. Behavioural markers of nonconscious face recognition in typical adults reflect a related phenomenon. Stone and Valentine (2005) simultaneously presented pairs of famous and unfamiliar faces for 17 ms, followed by a mask. Stimulus presentation time of 17 ms is too short to allow conscious face recognition. However, despite a complete inability of participants to identify the presence of a famous face, higher accuracy was observed for a subsequent dot probe discrimination task when the dot probe appeared in the same visual field as the famous face. This suggests that visual attention was involuntarily oriented towards the location of the famous face in a pair, and that facial identity was thus pre-consciously recognized. However, attentional capture for famous faces was only found when they were subsequently positively evaluated (i.e., as good or neutral relative to evil). These, findings suggest that some aspects of facial identity can be processed without conscious awareness, and that attention is preconsciously oriented towards famous faces versus unfamiliar faces.

In summary, evidence from different lines of research suggests that visual information about facial identity can be encoded with very little or no visual attention or conscious awareness, and irrespective of current task demands. This suggests that the visual analysis of identity-specific facial cues operates to some extent in a mandatory fashion, even when faces are novel or have only been encountered very infrequently. However, the exact conditions under which face recognition processes operate in a fully obligatory or optional fashion are still unknown.

Neural mechanisms of visual attention in fusiform gyrus

Behavioural evidence suggests that some aspects of unattended faces, including individual identity, can be processed in a mandatory fashion. But what are the mechanisms by which selective attention modulates the activity of face-selective brain regions, such as the fusiform face area? Neural responses for attended as compared to unattended faces can either be indistinguishable (fully mandatory processing), greater for attended than unattended stimuli (partial mandatory processing) or can be completely absent for unattended faces. Findings from functional brain imaging research suggest that neural responses of those regions that are involved in the processing of a particular stimulus are greatly reduced or even suppressed in the absence of selective attention (e.g., Kastner, de Weerd, Desimone, & Ungerleider, 1998). Others (e.g., Haxby et al., 1994; Wojciulik et al., 1998) showed that the degree of neural activation in face-selective regions is strongly modulated by the degree of attention towards faces or by their task relevance. When observers made explicit responses to faces, neural activity in face-selective regions was significantly enhanced as compared to a reduction in neural activation when faces were task-irrelevant. Similarly, Vuilleumier et al. (2001) reported bilateral increases in FFA activity when attention was directed to faces irrespective of their expression, and FFA activity in the right hemisphere was further increased when faces were fearful. These findings indicate that the strength of the FFA response depends on the allocation of selective attention to task-relevant face stimuli.

Effects of attention on face processing have also been observed for event-related brain potentials (ERPs) sensitive to faces. Consistent with fMRI findings, attended relative to unattended faces elicit enhanced neural responses of early face-selective components (e.g., Eimer, 2000a; see also Holmes, Vuilleumier, & Eimer, 2003). For example, Eimer (2000a) reported enhanced posterior amplitudes in the 135-180 ms post-stimulus time window (N170 latency range) to attended as compared to unattended face stimuli, demonstrating that visual attention strongly modulates face processes during early structural encoding (see Bruce & Young, 1986). Similar attentional modulations have also been observed for subsequent repetition-related ERP components (N250r). Trenner et al. (2004) directly investigated the influence of strategic processing on N250r amplitudes. ERP responses were recorded to famous face repetitions while participants performed two tasks: The *direct* task required explicit face identity matching of two sequentially presented faces, whereas the *indirect* task involved semantic judgments (i.e., actor or singer) to the second face in each pair. Results

showed that the N250r was significantly larger in the *direct* relative to the *indirec*t task, demonstrating a strong influence of selective attention on familiar face recognition. However, even though the N250r was reliably larger and more sustained for the *direct task*, this component was not completely absent for the *indirect task*, suggesting that some task-irrelevant information about the identity of the first irrelevant face had been processed automatically. Further evidence for mandatory face recognition comes from Schweinberger et al. (2004). In this study, reliable N250r repetition effects were observed for repeated unfamiliar faces under conditions where participants responded to infrequent butterfly targets. Even though identity was completely irrelevant during the search for target stimuli, the presence of an N250r to repetitions of the same face indicated that some information about unfamiliar face identity had been extracted. These findings suggest that explicit attention to faces or their identity is not required to form a perceptual memory trace of a previously seen face that can be immediately re-activated when the same person is seen for the second time.

A related question about the relationship between attention and individual face recognition has been addressed in a series of studies investigating the influence of perceptual load on incidental task-irrelevant face recognition. Neumann and Schweinberger (2008) tested whether directing attention away from famous faces during a letter detection task would interfere with the recognition of these faces. Two images (prime and probe) were presented in succession on each trial. Both images showed famous faces, but prime images consisted of letter strings superimposed on famous faces. Results showed that repeated presentations of famous faces triggered a clear N250r during letter identification, and the magnitude of this effect was unaffected by high or low perceptual load (i.e., observers either identified a target letter among 6 different or 6 identical letters). A second study by Neumann and Schweinberger (2009) showed that N250r components were also elicited to famous faces when small images of either buildings or unfamiliar faces served as distracters. These results suggest that the identity of task-irrelevant famous faces is incidentally processed during object detection tasks, indicating that the underlying neural mechanisms are to some extent activated in an automatic fashion. Overall, the findings provide evidence for a degree of mandatory (and thus not fully optional) identity processing, even under conditions where attention is directed away from faces or their identity.

Research aims

Experiment 3 examined the mechanisms of visual attention on individual face recognition, as reflected by the N250r component. More specifically, it was tested whether N250r components would be elicited to unfamiliar face repetitions in a task requiring relational but identity-unrelated judgments about the view in which two faces were shown. Participants performed same/different view judgments on sequentially presented face pairs, irrespective of whether these faces showed the same or two different individuals. This task was chosen, as it requires identity-unrelated face matching processes. Importantly, it directs attention towards the view in which a face is presented, while identity is task-irrelevant. However, participants are required to form a visual memory of the view of the first face, which can then immediately be re-activated when the second face is shown.

If the N250r was strictly dependent on intentional processing of identity, this component should be absent under conditions where identity is task-irrelevant. Alternatively, if observes cannot represent the view of a face without simultaneously representing its identity, a clear N250r component should be elicited in a view-matching task despite the fact that view and not identity was the attended feature. Task procedures were identical to those of the identity-matching tasks in Experiments 1 and 2, except that view was now the to-be-matched feature.

5.1.2 Method

Participants

Twelve paid volunteers (nine females), aged 24 to 37 years (mean age 30 years, SD = 5) were tested. All were right-handed, had normal or corrected-to-normal vision, and gave written informed consent.

Stimuli and procedure

The stimulus set contained naturalistic photographs of 30 unfamiliar individuals (15 female faces) taken from the FEI face database (http://fei.edu.br/~cet/facedatabase.html). These faces were converted into greyscale and cropped into an oval shape using Adobe Photoshop 6.0 (Adobe Systems Inc.). Images were shown either in a front view or in a right-facing side view at an angle of approximately 45° (see Figure 5.1). The view of the second face was randomized within each block. Stimulus size was 6.9° x 4.3° for the first face of each pair and

8.0° x 5.2° for the second face, and the average luminance of these face stimuli was 7.7 cd/m^2. Faces were presented centrally against a light grey background (16.5 cd/m^2). The combination of 30 different identities, two different views and two different sizes resulted in a total of 120 images. All stimuli were presented centrally on a CRT monitor at a viewing distance of 100 cm. E-Prime software (Psychology Software Tools, Pittsburgh, PA) was used for stimulus presentation and data collection.

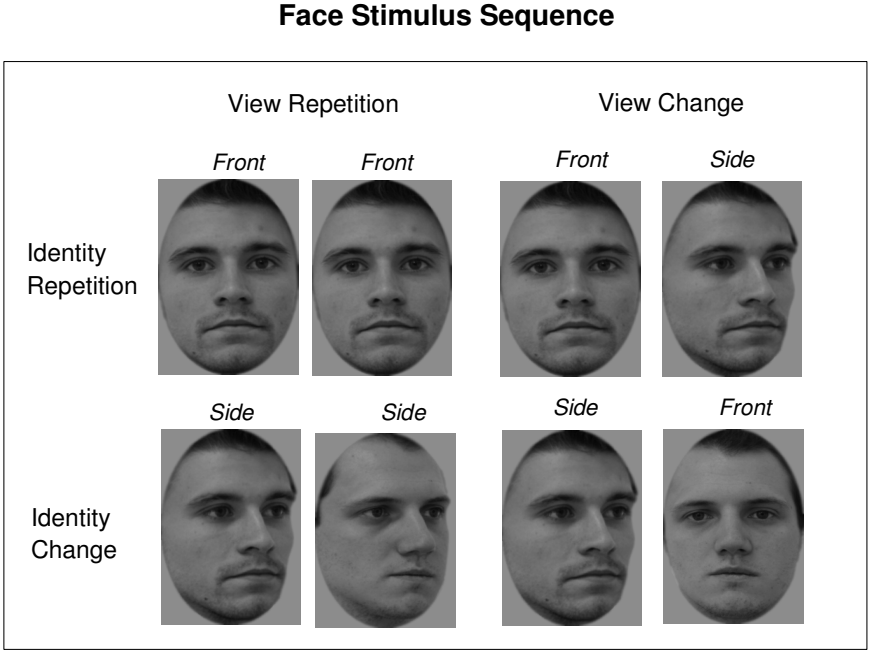


Figure 5.1 Examples of naturalistic face stimuli and the four different face stimulus sequences. Two faces showed either the same or two different persons (identity-repetition versus identity-change), in either the same view (front-front or side-side trials; view repetition) or a different view (front-side or side-front; view change). The second image was always 20% larger than the first image. Temporal parameters of stimulus presentation were identical to previous experiments.

Temporal parameters of stimulus presentation were identical to those used in previous experiments. Two faces were presented for 200 ms each, separated by a 200 ms interstimulus interval. The intertrial interval lasted for 1500 ms. Participants performed a view-matching task. They were instructed to respond with a left-hand button press on trials where the same view was repeated, and with a right-hand button press to view changes, regardless of whether the two faces showed the same or two different individuals. In all other respects, the design was identical to previous experiments. For purpose of analysis, view-repetitions were

collapsed across side-side and front-front trials, and view-changes were collapsed across front-side and side-front trials. Eight blocks were run with 80 trials each (20 for each combination of identity and view). The experiment lasted approximately 25 min, and participants performed one training block prior to testing.

EEG recording and data analysis

These were identical to Experiment 2, except that EEG was now also recorded from an additional inferior posterior electrode pair (electrodes P9 and P10). Mean amplitude values were computed at posterior electrodes P7/8 and P9/10 for the N170 time interval (160-190 ms after the onset of the second face) and for the N250r time interval (210-260 ms after the onset of the second face). Repeated-measures analyses of variance (ANOVAs) were performed for factors identity (identity-repetition versus identity-change), and view (view-repetition versus view-change). Analogous analyses were also conducted at frontal electrode Fz.

5.1.3 Results

Behaviour

Mean accuracy in the view-matching task was 91%. There were no reliable main effects of identity ($F(1,11) = 3.7$; $p > .08$) or view ($F(1,11) = 2.7$; $p > .13$) on accuracy. Mean RT was 557 ms. Responses were faster on trials where neither identity nor view changed (512 ms) than on trials where identity, view, or both attributes differed (573 ms, 576 ms, and 569 ms, respectively). This was reflected by significant or almost significant effects of identity ($F(1,11) = 27.8$; $p < .001$) and view ($F(1,11) = 4.5$; $p < .06$) and a highly significant view x identity interaction ($F(1,11) = 56.8$; $p < .001$).

ERP markers of visual face memory

Figure 5.2 (top panel) shows ERPs triggered by the second face in each pair on identity-repetition and identity-change trials at lateral occipital electrodes P7/8 and P9/10, and at frontal electrode Fz, averaged across all blocks. N250r components were clearly present in this view-matching task, and these showed the characteristic scalp topography with an enhanced posterior negativity which was accompanied by a frontal positivity to same face repetitions (see Figure 5.2, bottom panel). Figure 5.3 shows ERPs for identity repetitions

versus changes, separately for view-repetition (top panels) and view-change trials (bottom panels), demonstrating that a reliable N250r was elicited on both types of trials.

There was no reliable effect of identity on N170 amplitudes ($F(1,11) = 2.7$; $p > .12$), confirming findings of Experiments 1 and 2. Main effects of identity were present in the N250r time window (210-260 ms after the onset of the second face) at P7/8 ($F(1,11) = 7.9$; $p < .02$) as well as at P9/10 ($F(1,11) = 9.6$; $p < .02$), reflecting the presence of a reliable N250r component in this view-matching task. There were no reliable identity x view interactions at either of these two electrode pairs ($F(1,11) = 1.6$ and 3.3; $p > .22$ and .09, for P7/8 and P9/10, respectively), again suggesting that the N250r was largely view-independent. Follow-up one-tailed t-tests confirmed the presence of reliable N250r components on view-repetition trials ($t(11) = 2.5$ and 3.0; both $p < .02$, for P7/8 and P9/10, respectively) as well as on view-change trials ($t(11) = 2.1$ and 2.4; both $p < .04$, for P7/8 and P9/10, respectively). At anterior midline electrode Fz, a main effect of identity ($F(1,11) = 6.3$; $p < .03$) was due to an enhanced positivity for identity-repetition as compared to identity-change trials in the N250r time window. However, as reflected by an interaction between identity and view ($F(1,11) = 7.3$; $p = .021$), this differential effect was more pronounced and reliable on view-repetition trials ($t(11) = 2.8$; $p < .02$), but was not significant on view-change trials ($t(11) = 1.4$; $p > .18$).

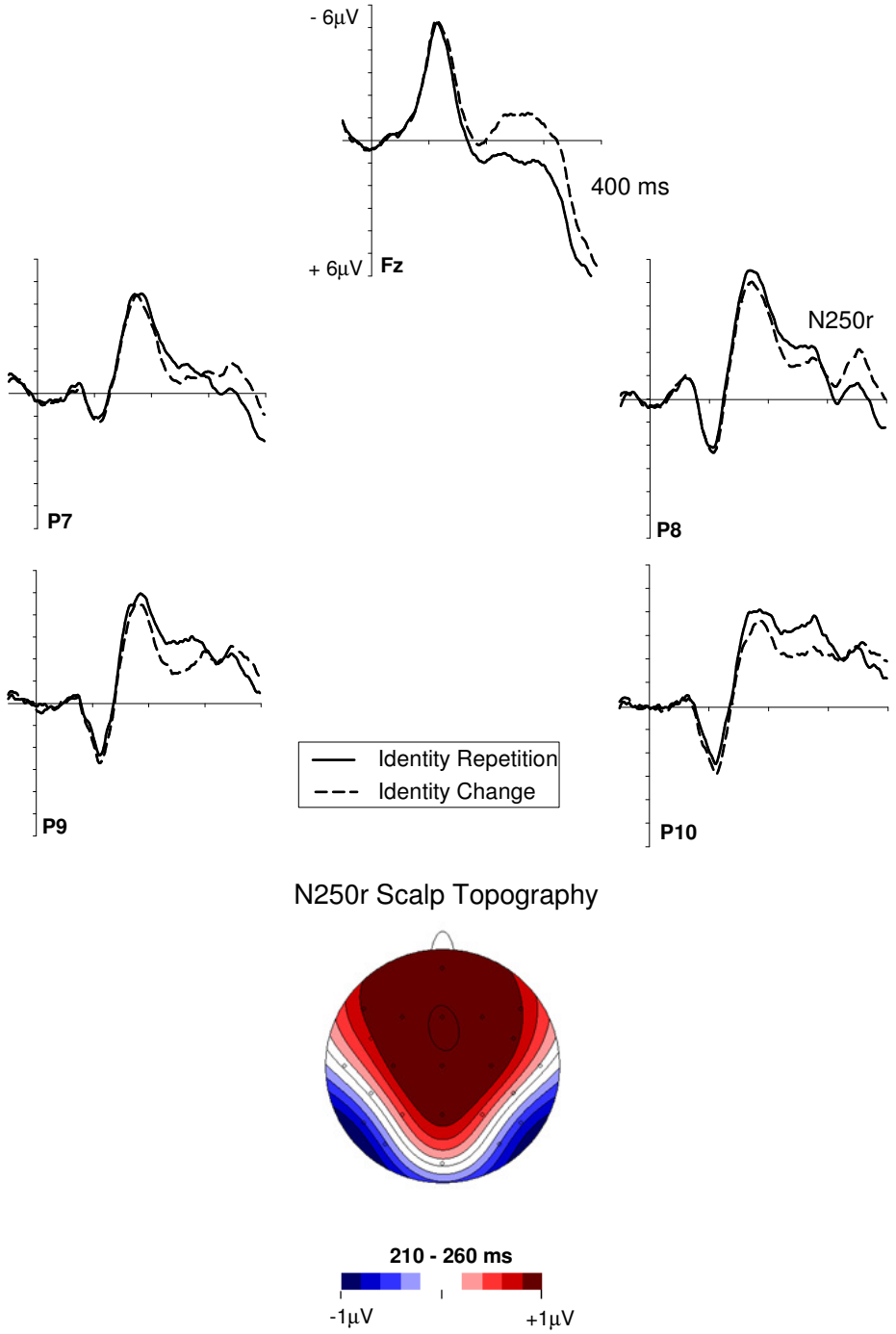


Figure 5.2 Top panel: Grand averaged ERP waveforms obtained at lateral posterior electrode pairs P7/8 and P9/10 and anterior midline electrode Fz in the 400 ms interval after the onset of the second stimulus in a face pair for identity-repetitions (solid lines) and identity-changes (dashed lines) during view-matching. Bottom panel: Scalp topography of N250r difference waves in the 210-260 ms post-stimulus time window, computed by subtracting ERP mean amplitudes on identity-change from ERP mean amplitudes on identity-repetition trials.

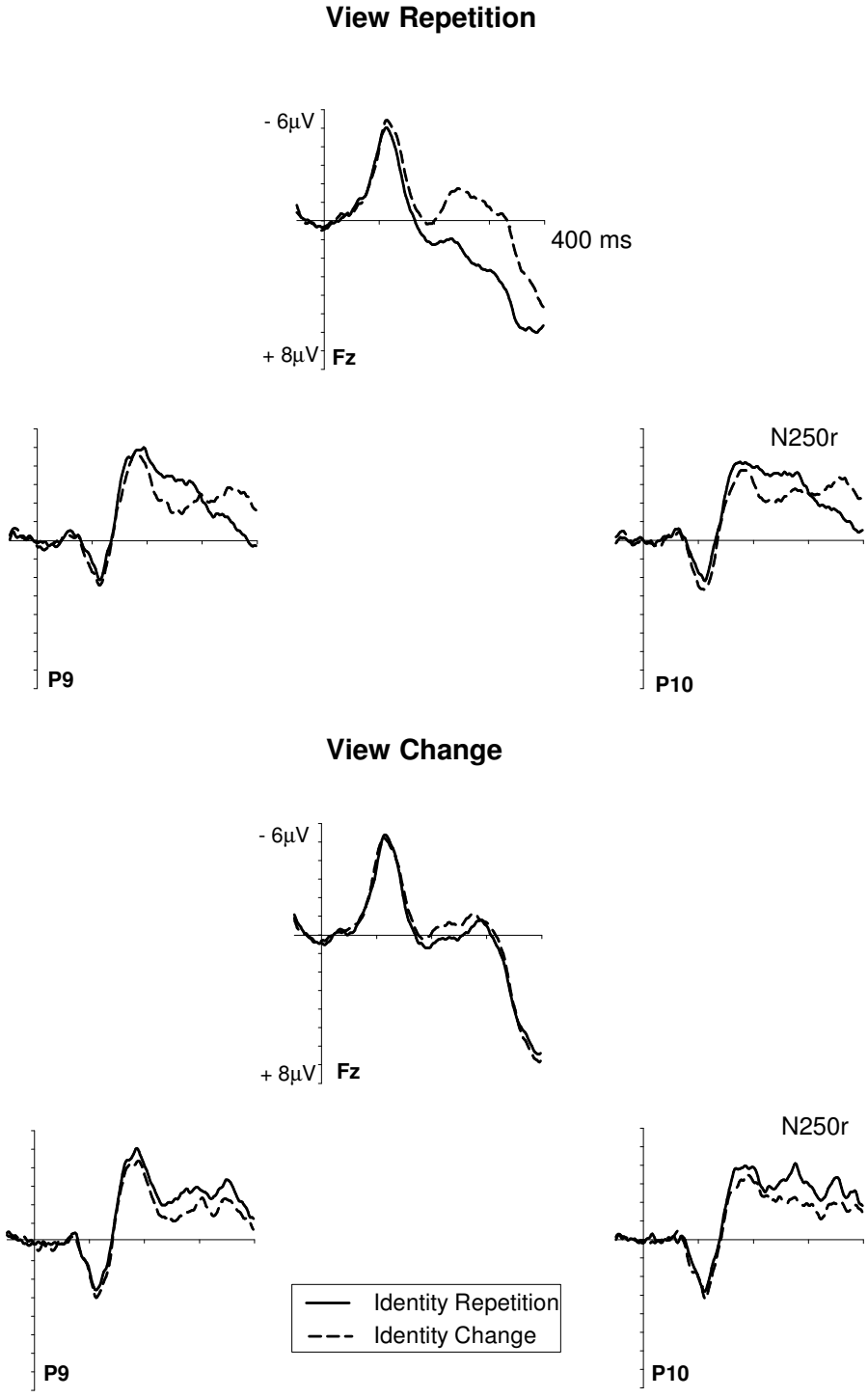


Figure 5.3 ERP waveforms obtained at posterior electrode pair P9/10 and anterior midline electrode Fz in the 400 ms interval after the onset of the second stimulus in a face pair for identity-repetition trials (solid lines) and identity-change trials (dashed lines) in a view-matching task, shown separately for view-repetition (top panels) versus view-change trials (bottom panels).

5.1.4 Discussion

To assess whether a relational judgment between two faces is critical for forming a memory of facial identity, ERPs were measured during a view-matching task. Reliable N250r repetition effects emerged, suggesting mandatory processing of unfamiliar face identity in a task requiring the formation of an explicit memory trace. The observation that face recognition processes were not only activated during explicit face identity judgments (as shown in Experiments 1 and 2), but also when view was the to-be-matched feature indicates that a fine-detailed visual memory trace of an individual face was encoded in a task-unrelated fashion. This was the case even though the present study employed a rapid repetition paradigm, where two faces appeared on the screen for 200 ms each, separated by a 400 ms interstimulus interval. Considering these rapid stimulus onset asynchronies (SOA), the presence of an occipito-temporal N250r to same face repetitions suggests that the underlying face recognition processes operate very rapidly and effortlessly.

A review of the existing literature yields inconsistent findings as to whether identity-specific processing is fully task-dependent and voluntary or operates in a strictly mandatory task-independent fashion. Humans are experts in discriminating hundreds of familiar faces, and the ease with which we distinguish a friend's face from that of a stranger suggests that the underlying face recognition processes operate in a rapid, effortless and thus automatic fashion. However, our expertise in face identification only applies to faces we are highly familiar with, and thus contrasts with recognition memory for unfamiliar faces, which is in comparison rather poor (e.g., Hancock et al., 2000). Therefore, it has been suggested that identity-specific processing for unfamiliar faces requires effortful and intentional processing and the need for attentional resources. Contrary to this assumption, the current findings provide evidence for mandatory processing of facial identity even when faces are unfamiliar, and do not activate rich representations of individual faces in long-term memory that have been formed for familiar individuals. This is in line with previous findings from different experimental paradigms suggesting that some information about the identity of to-be-ignored or task-irrelevant faces is processed regardless of the fact that novel unfamiliar face stimuli were used (e.g., Boutet et al., 2002; Schweinberger et al., 2004).

When comparing onset latencies and scalp topographies of the N250r repetition effects elicited in the view-matching task of Experiment 3 and in explicit face identity matching tasks in Experiments 1 and 2, it becomes apparent that the functional properties of the N250r were

very similar across experiments. This suggests that intentional and incidental face recognition processes share very similar underlying neural mechanisms. In other words, the present data do not suggest fundamental differences between explicit and implicit face recognition in tasks requiring the formation of an explicit memory trace. Another notable finding of Experiment 3 was that the size of the N250r did not reliably differ between view-repetition and view-change trials. This not only confirms analogous observations of view-independence of unfamiliar face recognition from Experiments 1 and 2 during explicit unfamiliar face identity-matching, but provides further evidence that unfamiliar face recognition operates in a view-independent fashion, even under conditions where identity encoding is task-irrelevant and thus incidental. This further implies that the obligatory encoding of facial identity in a view-matching task does not primarily involve low-level pictorial features, but mainly more abstract view-independent structural cues.

What was the common feature that was shared between the view-matching task of the present experiment and the identity-matching tasks of Experiment 1 and 2? Both tasks required relational same/different judgments with respect to a particular feature that was either repeated or alternated between two faces in a pair. In all of these tasks, a specific to-be-matched attribute of the first face had to be encoded and stored in visual working memory, and this newly formed memory trace was immediately re-activated in response to the second face. The presence of a reliable N250r in Experiment 3 where view and not identity was the attended feature demonstrates that the necessity to encode a visual feature of an unfamiliar face was sufficient for the simultaneous encoding of its identity. In this context, it would be interesting to test whether identity-specific processing is also mandatory for relational judgements about other types of facial cues, such as a person's expression. If forming an explicit perceptual memory trace contains identity-related facial cues by default, N250r components should emerge automatically across different face matching paradigms, irrespective of the nature of the attended facial attribute. This would emphasize the critical role of visual memory for the instantaneous representation of identity-specific visual information, and will need to be further assessed in future studies.

The stimuli choice of computer-generated colour images in previous experiments (Experiments 1 and 2) ensured a high level of visual similarity in terms of diagnostic facial features. By contrast, greyscale images of naturalistic faces were chosen in Experiment 3 to test whether the same functional properties also apply to physically more dissimilar and thus

more natural face stimuli. Despite their visual differences, both stimuli sets reliably elicited image-invariant N250r components, thereby highlighting that this component reflects the encoding of identity-specific information from a face. Moreover, the fact that latency and scalp topography of the N250r were very similar across experiments indicates that it generalizes across different types of face formats. Thus, the human face recognition system generalizes across a range of face or face-like stimuli as long as they conform to a general face template. This is in line with previous evidence of similar yet attenuated N250r components following stimulus repetitions across a variety of face or face-like stimuli (Schweinberger et al., 2004). It should be noted that in contrast to the explicit identity matching tasks of Experiments 1 and 2, the anterior counterpart of the N250r (an enhanced positivity for identity repetitions) was now reliably larger for view-repetition than for view-change trials (see Figure 5.3). This apparent dissociation between the posterior and anterior aspects of the N250r component in Experiment 3 may suggest that they do not reflect exactly the same underlying neural processes, and will need to be clarified in future studies.

In summary, the aim of the present study was to investigate whether the visual mechanisms that underlie unfamiliar face recognition are strictly mandatory or task-set dependent. Clear N250r components emerged to repetitions of unfamiliar faces in a view-matching task where identity was task-irrelevant, but a relational judgment between two faces was required. This suggests that the formation and retention of an active visual memory trace may be critical for mandatory identity processing, indicating that unfamiliar face recognition processes show a considerable degree of automatic (and thus not fully optional) processing of identity-related facial cues. To further clarify the effects of attention on individual face recognition, Experiments 4 and 5 compared N250r amplitudes during *explicit* and fully *implicit* tasks where not even a relational judgment about an identity-unrelated feature was required.

Chapter 6. Effects of task relevance and familiarity on face identity processing

Findings from Experiment 3 have shown that unfamiliar face identity is encoded in a mandatory fashion irrespective of selective attention and/or task demands in a view-matching task where observers made relational judgments about two sequentially presented faces. This suggests that even under conditions where information about the identity of a face is task-irrelevant, identity-specific facial cues are encoded in visual memory in an instantaneous and obligatory fashion. In other words, participants could not represent the view of a face without simultaneously representing its identity, as reflected by N250r responses to same face repetitions when view was the to-be-matched facial feature. The observation of mandatory identity processing in a task requiring explicit visual memory processes raises questions about the specific conditions under which identity processing is obligatory. Is the perception of unfamiliar face identity also fully mandatory in a task that does not contain this memory component? To address this question, Experiments 4 and 5 compared N250r amplitudes during *explicit* and fully *implicit* tasks: face identity matching (*explicit*) or target detection (*implicit*). Experiment 4 used unfamiliar faces, while stimuli in Experiment 5 consisted of both famous and non-famous faces to assess whether attention to faces is differentially modulated by their familiarity.

6.1 Experiment 4. Task-dependent face recognition and the role of visual face memory

6.1.1 Introduction

Previous research has shown that both unfamiliar and familiar faces are recognized unintentionally across a variety of different tasks for which identity is irrelevant, such as simple object detection tasks where participants need to detect butterfly targets (e.g., Schweinberger et al., 2004), or identify target letters (e.g., Neumann & Schweinberger, 2008, 2009). In these two paradigms, participants' task was to respond to objects other than faces, while trials consisted of either repetitions or non-repetition of images of the same famous celebrity. Even though there was no need to encode facial identity, N250r repetition effects were reliably obtained to repetitions of the same individual face, irrespective of task demands and irrespective of whether images showed faces of famous celebrities or unfamiliar

individuals. However, repetitions of identical images were used in these studies. To test whether the recognition of unfamiliar faces is mandatory under conditions where repeated face stimuli are shown in different views, Experiment 4 was conducted.

Research aims

Experiment 4 investigated whether unfamiliar face recognition processes operate in a mandatory task-independent fashion under conditions where the task does not require a relational judgment between two faces, but an immediate response to one of these faces only. N250r components to repeated unfamiliar faces were compared during two tasks: face identity matching (*explicit*) and target detection (*implicit*). In the *explicit* task, participants performed same/different identity judgments on sequentially presented face pairs. Two faces on each trial showed either the same, or two different persons, and either the same or two different views. In the *implicit* task, the experimental design was identical, except for added target trials showing inverted faces. On those target trials, either the first or the second face in a pair was inverted, and a response was required as soon as the target stimulus appeared on the screen. If unfamiliar face identity is processed in a mandatory fashion and independent of task requirements and/or demands on visual face memory, an N250r response of similar size should be observed in both *explicit* and *implicit* tasks. Alternatively, if identity-related face processing is task-dependent under conditions where immediate identity-unrelated responses to target faces are required, N250r responses should be strongly attenuated or absent for the *implicit* relative to the *explicit* task.

6.1.2 Method

Participants

Twelve paid volunteers (six females), aged 24 to 37 (mean age 25 years, SD = 5) were tested. All were right-handed, had normal or corrected-to-normal vision, and gave written informed consent prior to testing.

Stimuli and procedure

Face stimuli were identical to Experiment 2 (i.e., 12 computer-generated faces in full colour, shown in a full front or left-tilted side view), except that images of inverted face targets were included for the *implicit* task. Target stimuli were created by rotating each of the

12 facial identities by 180°. Image transformations were performed using Adobe Photoshop 6.0 (Adobe Systems Inc.). The combination of 12 target images in two sizes and two views resulted in a total of 48 stimuli. Participants performed two tasks that were presented in separate parts of eight consecutive blocks. The *explicit* face identity-matching task was identical to Experiment 2, except that the view of the second face was no longer constant within each block, but was randomized within each block. In the explicit task, there were eights blocks containing 80 trials each. There were 20 trials for view-repetitions (collapsed across front-front and side-side trials) and view-changes (collapsed across front-side and side-front trials), and 20 trials where two images showed the same person, and 20 trials where two different individuals were presented. In the *implicit* task, there were 16 additional target trials (1 trial for each combination of identity, view and target position: first or second image in a pair). Figure 6.1 illustrates exemplar target trials in the *implicit* task. Target trials made up 20% of all trials.

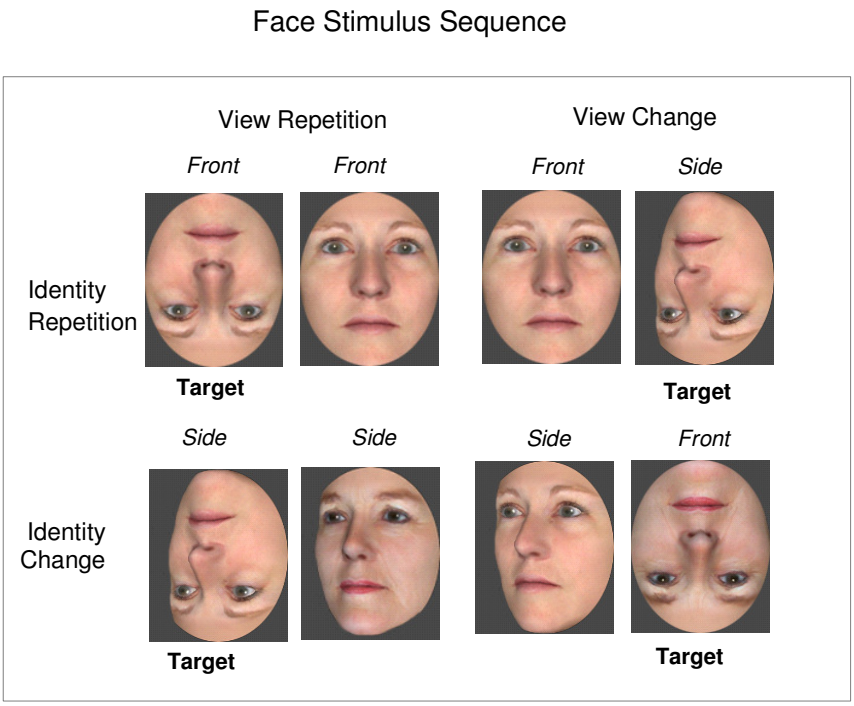


Figure 6.1 Examples of face stimulus sequences for target trials in the *implicit* task (inverted target detection) for four of the eight possible combinations of identity (identity-repetition versus identity-change), view (view-repetition versus view-change) and target position (first or second image). The second image was always 20% larger than the first image. Temporal parameters of stimulus presentation were identical to previous experiments.

There were 64 non-target trials (16 trials per condition) in each block for the *implicit* task. Participants were instructed to detect infrequent target stimuli (inverted faces) and to respond with a right-hand button press as soon as a target stimulus appeared on the screen. Targets could appear with equal probability as first or second stimulus in a pair. No response was required on those trials.

The remaining design was identical for both tasks: The factors identity and view were fully counterbalanced across trials, and identity-repetitions and view-repetitions made up half of all trials. Temporal parameters of stimulus presentation were identical to previous experiments, and task order was counterbalanced across participants. Two stimuli appeared on the screen for 200 ms each, separated by a 200 ms interstimulus interval. The intertrial interval was 1500 ms. Six participants started with the explicit face identity matching, while the remaining six performed the target detection task first. Each experimental task lasted approximately 25 minutes, and one training block was performed prior to the start of the first experimental block for each task.

EEG recording and data analysis

These were identical to Experiment 2. In the implicit task, only non-target trials where no response was recorded were employed for ERP analyses. These analyses included the additional factor task (explicit versus implicit). Mean amplitude values were computed at posterior electrodes P7/8 for the N170 time interval (160-190 ms after the onset of the second face) and for the N250r time interval (210-260 ms after the onset of the second face). Repeated-measures analyses of variance (ANOVAs) were performed for factors identity (identity-repetition versus identity-change), and view (view-repetition versus view-change). Analogous analyses were conducted at frontal electrode Fz.

6.1.3 Results

Behaviour

Explicit task. Mean accuracy for the identity-matching task was 92%. Participants were more accurate on same-identity judgments than on different-identity judgments (96% versus 89%; $F(1,11) = 9.9$; $p < .01$), and on view-repetition relative to view-change trials (95% versus 90%; $F(1,11) = 47.4$; $p < .001$). There was no identity x view interaction for accuracy ($F < 1$). Mean correct RT was 571 ms, and participants were faster for identity-repetition than

identity-change trials (539 ms versus 604 ms; $F(1,11) = 16$; $p < .01$) and for view-repetition than view-change trials (551 ms versus 591 ms; $F(1,11) = 59.5$; $p < .001$). A significant identity x view interaction ($F(1,11) = 32.3$; $p < .001$) demonstrated that RTs were significantly faster for same-identity judgments in the same versus different views (501 ms versus 577 ms) while RTs for different-identity judgments did not differ for same versus different views (602 ms versus 605 ms).

Implicit task. Participants accurately detected 95% of all inverted face targets. Mean RT was 505 ms, and there were no False Alarms on non-target trials.

ERP markers of visual face memory

Figure 6.2 (top panel) shows ERPs triggered by the second face stimulus in each pair on identity-repetition and identity-change trials at posterior occipital electrodes P7/8, separately for *explicit* and *implicit* tasks. Clear repetition effects were found for the explicit but not for the implicit task for both posterior and anterior N250r components, suggesting that this component was strongly modulated by task relevance and/or attentional focus. This was further illustrated by characteristic N250r scalp topographies for the explicit but not the implicit task, obtained by subtracting identity-change from identity-repetition trials (see Figure 6.2, bottom panel).

N170 amplitudes measured in the 160-190 ms time window were not modulated by identity ($F < 1$). In the N250r time window (210-260 ms after the onset of the second image), a main effect of identity ($F(1,11) = 9.0$; $p < .02$) was accompanied by a significant identity x task interaction ($F(1,11) = 15.6$; $p < .01$), demonstrating that N250r components were strongly modulated by task demands. Separate analyses for each task confirmed that reliable N250r components were elicited in the explicit task ($F(1,11) = 13.4$; $p < .01$) but not in the implicit task ($F < 1$). In line with previous findings, there was no identity x view interaction in the explicit task ($F(1,11) = 2.0$; $p > .19$), indicating that the N250r was view-independent. Follow-up one-tailed t-tests confirmed the presence of reliable N250r components on view-repetition trials ($t(11) = 3.34$; $p < .01$), as well as on view-change trials ($t(11) = 2.11$; $p < .03$).

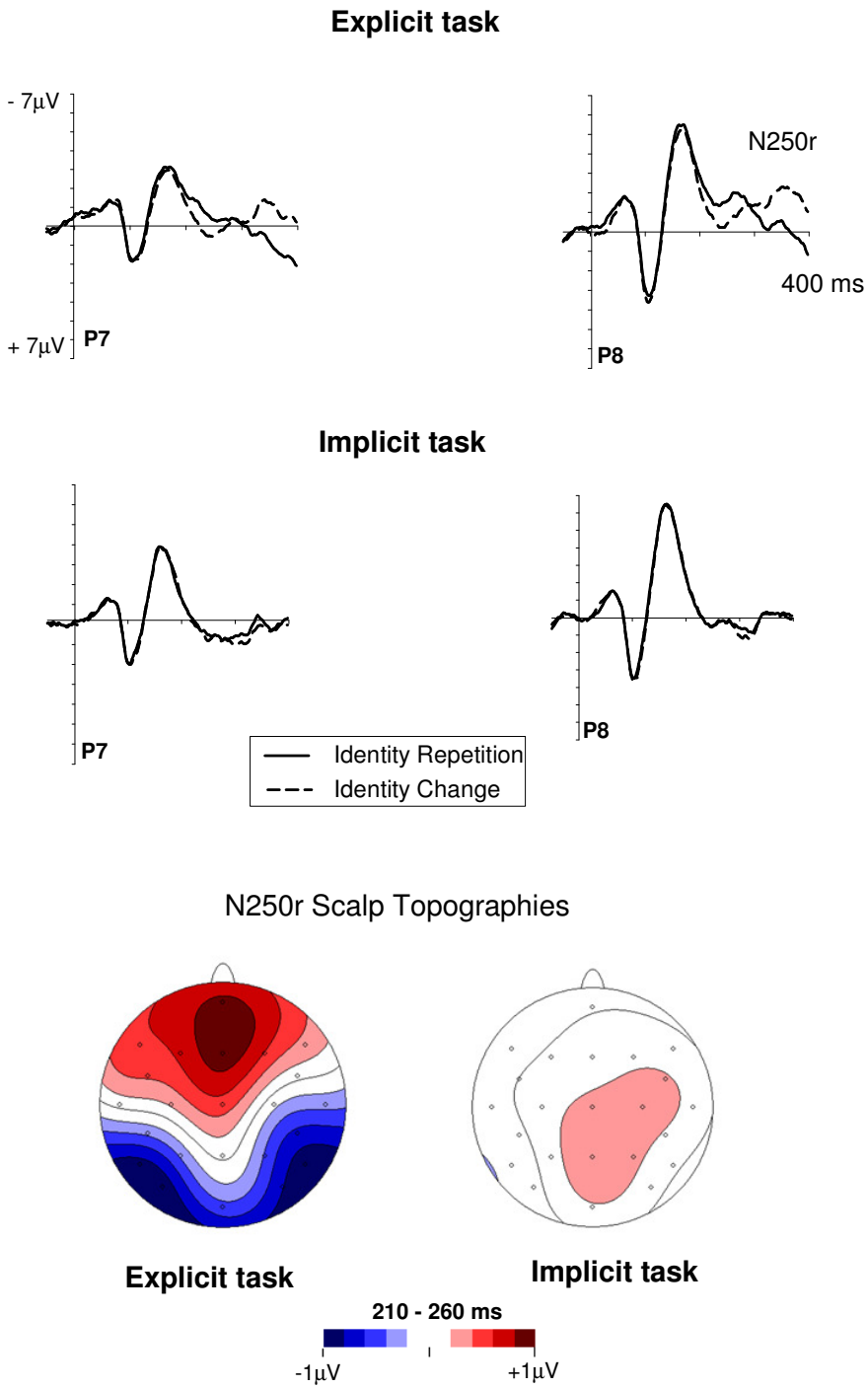


Figure 6.2 Top panel: Grand averaged ERP waveforms elicited at lateral posterior electrode pair P7/8 in the 400 ms interval after the second face in a pair. ERPs are averaged separately for identity-repetition trials (solid lines) and identity-change trials (dashed lines), and are shown separately for *explicit* and *implicit* tasks. Bottom panel: Topographic maps of N250r difference waves obtained by subtracting ERPs on identity-changes trials from ERPs on identity-repetition trials, shown separately for *explicit* and *implicit* tasks.

The posterior N250r was again accompanied by an anterior enhanced positivity for identity-repetitions as compared to identity-change trials ($F(1,11) = 7.9$; $p < .02$). A significant identity x task interaction was present at frontal electrode Fz ($F(1,11) = 13.4$; $p < .01$), and follow-up analyses confirmed the presence of reliable anterior identity repetition effects in the explicit task ($F(1,11) = 14.2$; $p < .01$), as well as a significant identity x view interaction ($F(1,11) = 6.0$; $p < .04$), while no such effects were present for the implicit task ($F < 1$). Follow-up one-tailed t-tests for the explicit task confirmed the presence of a reliable anterior N250r on view-repetition trials ($t(11) = 3.9$; $p < .01$), and its absence on view-change trials ($t < 1$).

6.1.4 Discussion

Experiment 4 tested whether unfamiliar face recognition processes are engaged in a mandatory fashion in an *implicit* task that does not require a relational judgment between two faces but an immediate response to inverted face targets. ERP waveforms were recorded during two tasks in which participants either matched the identity of two sequentially presented faces *(explicit)* or detected inverted face targets which infrequently appeared as either first or second image in a face pair *(implicit).* Consistent with previous findings, N170 components were unaffected by repetitions versus changes of identity. The critical question was whether systematic N250r repetition effects would emerge for same face repetitions not only for the explicit but also for the implicit task.

Results were clear-cut: A reliable N250r component was present over occipito-temporal regions for the explicit face identity matching task, but was absent for the implicit target detection task (see Figure 6.2, top panel). These findings demonstrate that neural processes for unfamiliar face recognition, as reflected by the N250r, are not triggered in a mandatory fashion but are abolished when observers search for infrequent targets (i.e., inverted faces). As in Experiments 1-3, an N250r was elicited by unfamiliar face repetitions in the explicit identity-matching task, and this component showed the expected scalp distribution with a posterior negativity accompanied by an anterior positivity (see Figure 6.2, bottom panel). In spite of the fact that stimulus parameters were identical for the explicit task and for non-target trials in the implicit task, the N250r was completely absent in this task, demonstrating that the underlying mechanisms are strongly task-set dependent.

The absence of the N250r in the implicit target detection task, and its presence during implicit view matching in Experiment 3 could be interpreted as evidence that unfamiliar face

identity is processed in an automatic fashion only if the task requires actively holding a facial attribute in visual working memory. Thus, the mandatory processing of unfamiliar face identity appears to depend on the need to maintain information about the first face image in visual memory, which is then immediately matched with the second image. This task-relevant information can be unrelated to identity, as was the case in Experiment 3 where view was the attended facial feature. These findings are consistent with fMRI evidence showing that face recognition is strongly modulated by task-dependent factors and thus not strictly mandatory (e.g., Haxby et al., 1994; Wojciulik et al., 1998). Likewise, strong attentional modulations have also been observed for ERP markers of visual face memory (N250r components; e.g., Trenner et al., 2004). It remains unclear from the present data whether visual attention is required for the initial perception of an individual face and/or subsequent neural processes for the formation of a perceptual face representation in short-term memory. In other words, it cannot be ruled out that identity-specific visual cues were immediately processed in the implicit task, but that this information was not actively held in visual working memory, and therefore did not elicit an N250r response.

At first glance, the present results appear to contradict findings from Schweinberger et al. (2004) of N250r repetition effects to unfamiliar face repetitions during a butterfly detection task. One possible explanation for this discrepancy may relate to differences in the temporal parameters of stimulus presentation. The present study employed a rapid repetition paradigm where two faces appeared on the screen for 200 ms each, separated by a 200 ms interstimulus interval. In contrast to the 400 ms SOA in Experiment 4, Schweinberger et al. presented each face stimulus for 1 second with an SOA of 2 seconds. This prolonged exposure time may have resulted in more detailed processing of subtle individual differences, resulting in mandatory encoding of facial identity. Thus, acquiring visual memories for individual faces when temporal task demands are high may require considerable effort and therefore selective attention. If this interpretation is correct, longer exposure times may lead to the incidental representation of facial identity in visual working memory, and exposure time may be one of the critical determinants that decide whether or not identity-specific processing is obligatory. This will need to be clarified in future research.

The aim of Experiment 4 was to test whether unfamiliar face identity is extracted in a task-independent and thus obligatory fashion during an *implicit* target detection task. Previous research has yielded inconsistent results as to whether or not the processing of unfamiliar

face identity is mandatory (e.g., Boutet et al., 2002; Khurana et al., 2000). Taken together, the findings from Experiments 3 and 4 suggest that identity-related processing is neither fully mandatory nor fully task-set dependent: The identity of unfamiliar faces is encoded in a mandatory fashion in tasks that require the maintenance of face-specific visual memory traces for individual faces, but can be completely ignored during tasks that do not have this memory component. Thus, results show that the requirement to encode an individual's face in visual memory determines whether or not identity-related information is instantaneously stored, regardless of task sets and/or attentional focus.

If identity-specific facial cues were not encoded during the search for face targets (*implicit*), what types of neural processes were engaged in this task? Theoretically, this task could have been achieved by detecting visual changes in the global face layout (i.e., in its simplest form detecting two eyes above a mouth). In Bruce and Young's (1986) model, this would relate to the earliest stage of visual analysis (i.e., structural encoding) prior to the detailed analysis of subtle variations in facial cues that allow face identification. Thus, implicit and explicit tasks may require different levels and/or depths of visual processing, which involve either the basic perception of a generic face template (*implicit*), or a deeper level of identity-related face processing (*explicit*). Alternatively, the perception of an individual's unique visual features may be mandatory, but not the formation and retention of an explicit face memory trace. In other words, visual processing of identity-specific facial information may be obligatory, but this information fades away instantaneously unless it is actively hold in working memory. Future research is needed to distinguish between these two possible interpretations.

In summary, the findings from Experiment 4 demonstrate that unfamiliar face recognition processes are fully optional and task-dependent (and thus not mandatory) under conditions where stimuli are presented at rapid SOAs and the task requires searching for inverted face targets. Results further suggest that the requirement to form an explicit face memory is critical, and may determine whether task-irrelevant identity is encoded. Thus, even though the acquisition of face representations is under some conditions fully mandatory (see Experiment 3); the same neural processes are to a considerable extent task-set dependent during tasks that do not contain a memory component.

6.2 Experiment 5. The role of attention for the perception of familiar face identity

6.2.1 Introduction

The findings from Experiment 4 suggest that the perception of unfamiliar face identity is not fully mandatory but under certain conditions dependent on task relevance and/or visual attention. More specifically, when there is no need to encode identity-related information from a face, perceptual memories of unfamiliar faces are not actively maintained. The question arises whether familiarity with a face modulates the degree to which face identity processing relies on task-dependent attention. Is familiar face identity processed in a mandatory fashion in contrast to the observed dependence of unfamiliar face recognition processes on task relevance? In line with the proposed functional distinction between familiar and unfamiliar face processing (e.g., Hancock et al., 2000), one important difference in the underlying neural mechanisms might relate to the role of selective attention for the perception of individual identity. There has been little systematic research into the effects of selective visual attention on the neural processes associated with familiar as compared to unfamiliar face recognition. Although it appears intuitive that familiarity with faces aids their representation in visual working memory (WM), it is not clear whether familiarity with a face enables particularly efficient and/or mandatory processing of its identity. Many studies have shown that familiar faces have a processing advantage over unfamiliar faces and are more likely to attract attention, for instance during visual search tasks (e.g., Tong & Nakayama, 1999) or change detection paradigms (e.g., Buttle & Raymond, 2003). Likewise, familiarity with complex visual objects such as faces has also been shown to enhance visual WM performance (Jackson & Raymond, 2008), reflecting facilitated storage of items in WM if robust visual representations of them already exist in long-term memory. Unlike unfamiliar face recognition, the identification of familiar faces may benefit from the existence of stable representations for known faces. Therefore, it seems plausible to assume that the extent to which face recognition processes require attention may be related to the degree of previous exposure to an individual face and the formation of robust face memory representations over time.

Humans are highly skilled at discriminating individual faces, but this expertise only refers to the identification of highly familiar faces, and contrasts with poor recognition memory for

unfamiliar faces (e.g., Bruce, 1982). Recognizing unfamiliar faces is assumed to require effortful and controlled processing, in contrast to the ease with which familiar faces are distinguished (e.g., Burton et al., 1999). It thus seems likely that a salient stimulus (e.g., a famous face) attracts attention to a larger extent in an automatic fashion than a less salient stimulus (e.g., an unfamiliar face). If familiarity automatically directs attention to particular facial features including visual cues about identity, this should result in mandatory face identity processing. Surprisingly little research has addressed whether differences between familiar and unfamiliar face processing are partly attributable to differences in the role of visual attention for individual face recognition. The fact that our ability to recognize unfamiliar faces is much poorer than familiar face recognition suggests that there are systematic qualitative differences in the perceptual encoding or memory storage of familiar versus unfamiliar faces. Attention may therefore differentially modulate the perception of facial identity as well as the representation of an individual's face in WM, depending on whether or not a person is familiar. Memory representations are more robust for familiar than for unfamiliar faces, and it has been argued that familiar face recognition, and in particular the activation of rich visual memories of a familiar face, may be particularly hard to suppress (e.g., Ellis et al., 1990; Buttle & Raymond, 2003).

Research aims

Experiment 5 investigated whether the recognition of famous as compared to non-famous faces operates in a fully mandatory fashion, irrespective of task-dependent attention. Each participant performed two tasks: face identity matching (*explicit*) and target detection (*implicit).* Design and procedure of the two tasks were identical to Experiment 4, except that face stimuli in both tasks contained images of both famous faces (i.e., actors, politicians) and non-famous (i.e., unfamiliar) faces. In contrast to Experiments 1-3 where face stimuli were shown across different views, all images were now shown in a full front view only. If the processing of familiar as compared to unfamiliar face identity proceeds independently from attention and/or task demands, this should be reflected by systematic differences in N250r responses for *explicit* and *implicit* tasks, depending on whether famous or non-famous faces are seen More specifically, if the neural processes for famous face recognition operate in a task-independent (and thus automatic) fashion, N250r repetition effects should emerge for both *explicit* and *implicit* tasks when two images show a famous person.

6.2.2 Method

Participants

Twelve paid volunteers (five females), aged 22 to 35 (mean age 28 years, SD = 4) were tested. Data from two further participants were excluded due to an insufficient number of artifact-free EEG trials (less than 60% of all trials left after artifact rejection). All participants were right-handed, had normal or corrected-to-normal vision, and gave written informed consent prior to the experiment.

Stimuli and procedure

These were identical to Experiment 4 with the following exception: Stimuli now consisted of a complete new set of 30 naturalistic faces (15 female) including 15 images of unfamiliar faces (i.e., non-famous) and 15 images of famous faces taken from a stimulus set used by Gosling & Eimer (2011). The latter were celebrities widely known to the general public in the UK (i.e. actors/ actresses, politicians, members of the royal family). All face stimuli were shown in a full front view. For each of the 15 famous faces, one non-famous face was selected from a larger sample to provide a match in terms of gender, approximate age, facial expression (i.e., neutral or smiling) and low-level visual attributes such as contrast and brightness (see Figure 6.3, for stimuli examples). As in Experiment 4, target stimuli in the implicit task were created by rotating each of the 30 faces by 180°. The combination of 30 identities, 30 target stimuli and two different sizes resulted in a total of 120 different images in the *implicit* task. In the explicit task, there were 60 different images (no inverted faces). All stimuli were converted to greyscale, resized, and cropped into an oval shape, thereby removing their outer contours. These image transformations were performed in Adobe Photoshop CS3. All stimuli were presented at fixation against a light grey background (16.5 cd/m^2). They subtended a visual angle of 6.9° × 4.3° (first image) and 8.0° x 5.2° (second image) and their average luminance was 21.9 cd/m^2.

Face pairs either consisted of two famous or two non-famous faces so that face type was held constant within each trial. Eight experimental blocks were run for each task, which contained 80 trials each; 20 trials for each of the four combinations of identity (identity-repetition versus identity-change) and face type (famous versus non-famous). Target trials in the *implicit* task made up 20% of all trials and targets could appear with equal probability as first or second stimulus in a face pair. In the implicit task, each block consisted of 72 non-

target trials (18 trials per condition), and 8 target trials (1 trial for each combination of identity, face type and target position). Figure 6.3 shows examples of face stimulus sequences for non-target trials (top panel) and target trials (bottom panel). No response was required on non-target trials. The experiment lasted approximately 25 min, and participants performed two training blocks (one for each task) prior to testing.

Temporal parameters of stimulus presentation were identical to previous experiments, and task order was counterbalanced across participants. Two faces on each trial were presented for 200 ms, separated by a 200 ms ISI. The intertrial interval was 1500 ms. All other parameters were identical across both tasks, except that participants performed explicit familiarity judgments after completing both tasks, requiring famous/ non-famous judgments to each of the 15 famous and 15 non-famous faces. Each face stimulus was presented once for 600 ms, and was followed by an 800 ms blank interval after which the next face appeared on the screen. Participants' task was to respond with a left-hand button press to a famous face and with a right-hand button press to a non-famous face. Famous faces that were incorrectly classified as non-famous were initially excluded from the EEG analyses. However, analyses with and without unrecognized famous faces gave analogous patterns of results. Therefore, EEG analyses reported here are across all famous faces.

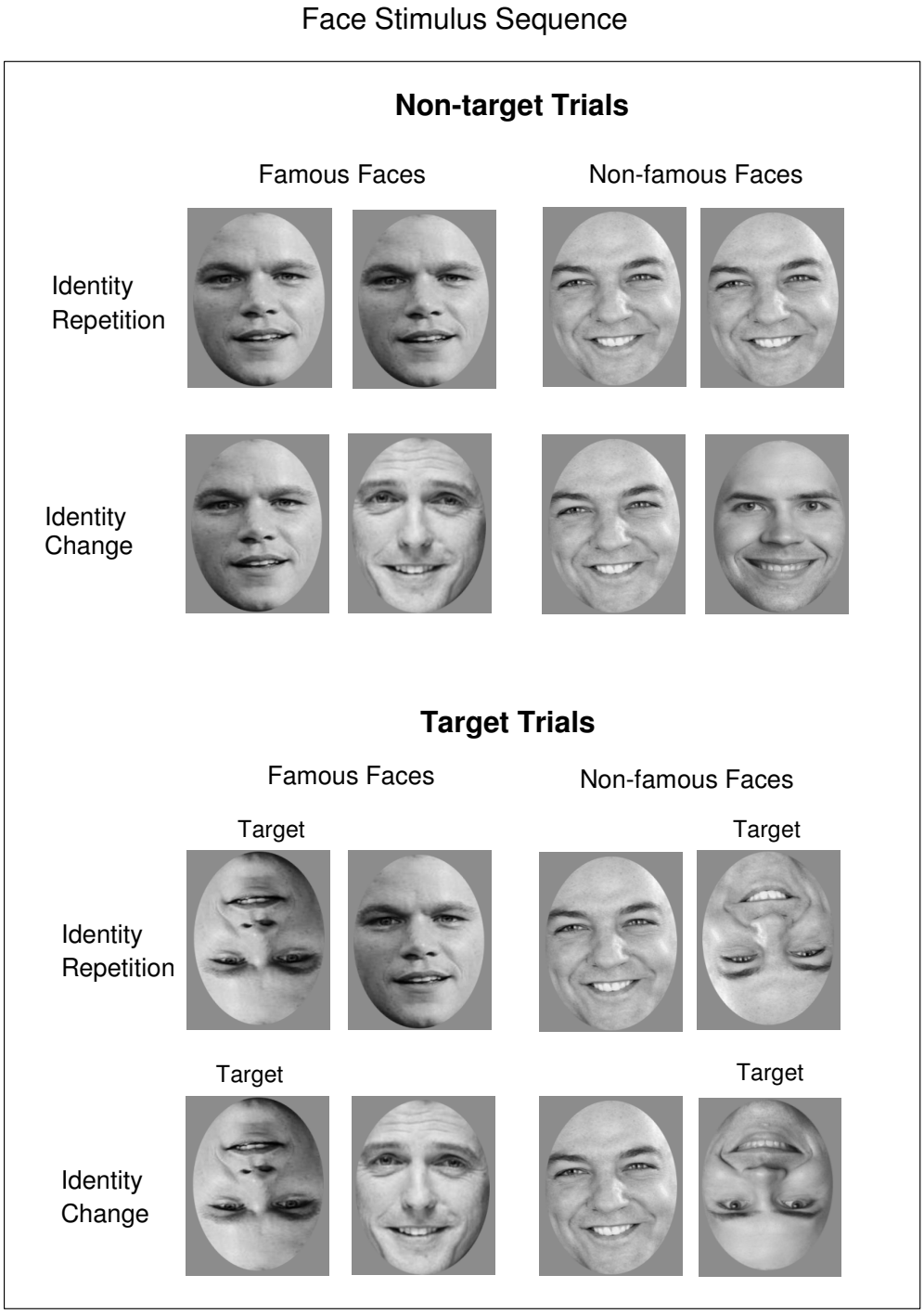


Figure 6.3 Top panel: Examples of different face stimulus sequences for non-target trials in *explicit* and *implicit* tasks for all combinations of identity (identity-repetition versus identity-change) and face type (famous versus non-famous). Bottom panel: Face stimulus sequences for target trials in the implicit task for four out eight possible combinations of identity, face type and target position (first or second image). Note that the second image was always 20% larger than the first image.

EEG recording and data analysis

These were identical to Experiment 4, except that EEG was also recorded from an additional inferior posterior electrode pair (electrodes P9 and P10) and analyses included the additional factor face type (famous versus non-famous). Mean amplitude values were computed at posterior electrodes P9/10 for the N170 time interval (160-190 ms after the onset of the second face) and for the N250r time interval (210-260 ms after the onset of the second face). Repeated-measures analyses of variance (ANOVAs) were performed for factors identity (identity-repetition versus identity-change), and face type (famous versus non-famous). Analogous analyses were also conducted at frontal electrode Fz.

6.2.3 Results

Behaviour

Explicit task. Overall accuracy for face identity matching was 98%. There were no main effects of identity (98% versus 97% for identity repetitions versus changes; F(1,11) = 2.9; p = .115), or face type (98% each; $F(1,11) = 1.6$; $p = .231$). There was also no reliable interaction between identity and face type ($F(1,11) = 3.5$; $p < .09$). Mean RT for correct trials was 440 ms. Participants were faster on identity-repetition than on identity-change trials (423 ms versus 456 ms; $F(1,11) = 12.5$; $p < .01$). Again, there was no main effect of face type (439 ms versus 440 ms for famous versus non-famous faces; $F < 1$), and no identity x face type interaction ($F<1$).

Implicit task. Participants accurately detected 99% of all inverted face targets regardless of face type (99% both for famous and non-famous faces). Mean RT was 420 ms, and there were no False Alarms on non-target trials.

Familiarity judgments. On average, participants correctly classified 81% of all faces, and familiarity judgments were more accurate for famous relative to non-famous faces (88% versus 73%). Mean RT was 611 ms, and RTs were faster for famous than non-famous faces (572 ms versus 650 ms).

ERP markers of visual face memory

ERPs triggered by the second face stimulus in each pair on identity-repetition and identity-change trials at lateral occipital electrodes P9/10 are shown separately for *explicit* and *implicit*

tasks, and for non-famous and famous faces (see Figures 6.4 and 6.5, top panels, respectively). Non-famous faces triggered clear N250r repetition effects for the *explicit* but not for the *implicit* task, replicating findings from Experiment 4. The exact same pattern also emerged on famous face trials: An N250r was triggered by same face repetitions for the *explicit* but not the *implicit* task, indicating that familiarity did not modulate the task-dependence of identity-related face processing. This is further illustrated by characteristic posterior negativities of N250r differences waves (obtained by subtracting identity-change trials from identity-repetition trials) for explicit but not implicit tasks for both non-famous and famous faces (see scalp topographies in bottom panels of Figures 6.4 and 6.5, respectively).

Consistent with findings from Experiments 1-3, there was no main effect of identity in the N170 time window (160-190 ms; $F < 1$). A main effect of identity emerged in the N250r time window for ERP data obtained at posterior electrodes P9/10 collapsed across tasks (210-260 ms; $F(1,11) = 6.8$; $p < .03$). There was no identity x face type interaction or three-way interaction (identity x task x face type: both $F < 1$). A significant identity x task interaction ($F(1,11) = 38.3$; $p < .001$) demonstrated that N250r responses were strongly modulated by task demands. Follow-up analyses were conducted separately for each task. For the *explicit* task, there was a main effect of identity ($F(1,11) = 34.7$; $p < .001$), but no interaction between identity and face type ($F < 1$), suggesting that an N250r of similar size was elicited for both famous and non-famous faces. For the *implicit* task, a main effect of identity was absent, and there was no identity x face type interaction (both $F < 1$), indicating that N250r components were absent for this task regardless of face familiarity.

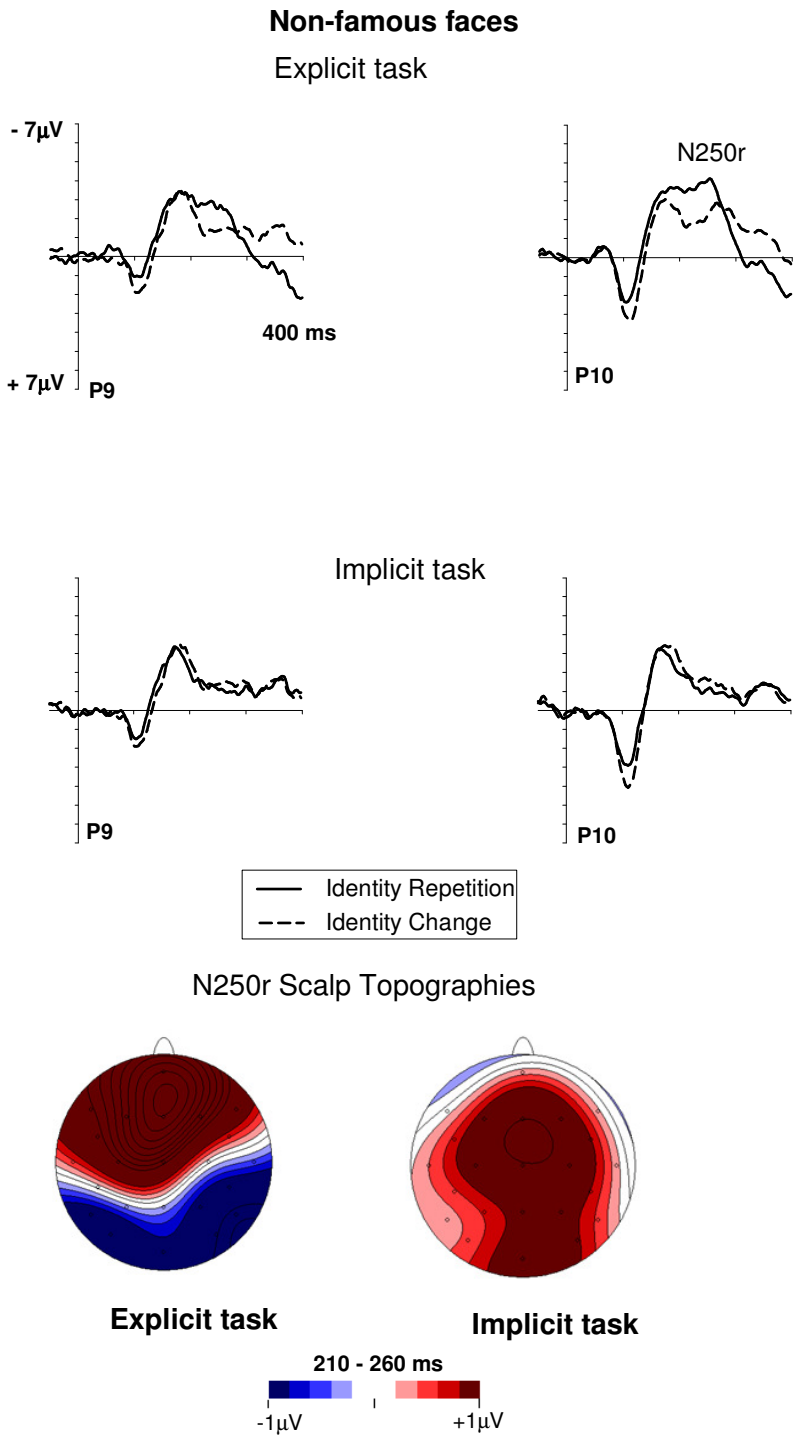


Figure 6.4 Top panel: Grand averaged ERP waveforms obtained at posterior electrode pair P9/10 in the 400 ms interval for non-famous faces for identity-repetition trials (solid lines) and identity-change trials (dashed lines), shown separately for *explicit* and *implicit* tasks. Bottom panel: N250r scalp topographies obtained by subtracting ERPs on identity-change from ERPs on identity-repetition trials for famous face repetitions, shown separately for *explicit* and *implicit* tasks.

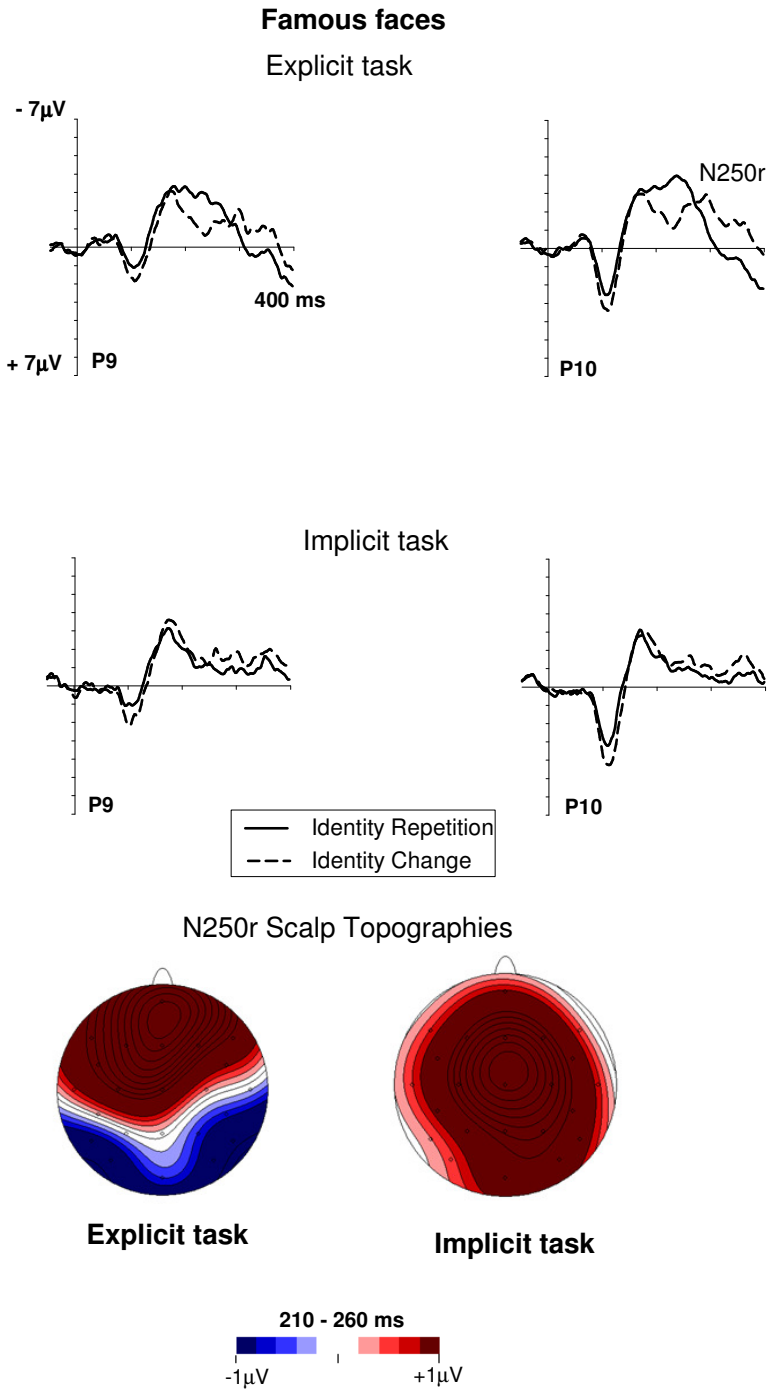


Figure 6.5 Top panel: Grand averaged ERP waveforms obtained at P9/10 in the 400 ms time window for famous faces on identity-repetition trials (solid lines) and identity-change trials (dashed lines). ERP data are shown separately for *explicit* and *implicit* tasks. Bottom panel: N250r scalp topographies obtained by subtracting ERPs on identity-change from ERPs on identity-repetition trials for repetitions of famous faces, shown separately for *explicit* and *implicit* tasks.

Separate follow-up analyses were also conducted for the factor face type. For non-famous faces, a main effect of identity approached significance ($F(1,11) = 5$; $p < .06$), and was accompanied by a significant identity x task interaction ($F(1,11) = 24.6$; $p < .001$), demonstrating that N250r amplitudes on those trials were task-set dependent. For non-famous faces, separate analyses for explicit and implicit tasks confirmed the presence of a reliable N250r component in the explicit task ($F(1,11) = 19.9$; $p < .01$), and its absence in the implicit task ($F < 1$). The same pattern of results was obtained for famous faces: Here, an N250r ($F(1,11) = 7.1$; $p < .03$) was accompanied by a significant interaction between identity and task ($F(1,11) = 27.5$; $p < .001$). Followed up analyses on ERP data obtained on famous face trials, separately for explicit and implicit tasks, showed strong task-set dependent N250r modulations. An N250r was reliably triggered by same face repetitions for the explicit task ($F(1,11) = 36.2$; $p < .001$), but again not for the implicit task ($F < 1$).

A different pattern of results emerged at anterior midline electrode Fz: Here, an enhanced anterior positivity was obtained for identity-repetition relative to identity-change trials ($F(1,11) = 17.3$; $p < .01$), but there was no identity x task interaction ($F(1,11) = 1.4$; $p = .265$), or three-way interaction (identity x task x face type: $F(1,11) = 2$; $p = .195$). Follow-up analyses conducted separately for each task demonstrated the presence of an anterior N250r not only for the explicit task ($F(1,11) = 15.7$; $p < .01$), but also for the implicit task ($F(1,11) = 8.4$; $p < .02$). Again, there was no effect of face familiarity on N250r amplitudes for either task (identity x face type; $F > 1$ and $F(1,11) = 2.9$; $p= 1.14$ for *explicit* and *implicit* tasks, respectively). Analogous analyses conducted separately for the factor face type confirmed significant main effects of identity for both famous faces ($F(1,11) = 11.3$; $p < .01$) and non-famous faces ($F(1,11) = 22.1$; $p < .01$), but there were no identity x task interactions for either type of faces ($F(1,11) = 2.9$; $p = 1.18$ and $F > 1$ for famous and non-famous faces, respectively).

6.2.4 Discussion

Experiment 5 tested whether familiarity with a face modulates strategic task-specific influences on identity-related processing. Previous research has suggested that functionally different neural mechanisms underlie the processing of familiar relative to unfamiliar faces for both the initial perception of unique identity and its representation in visual face memory (e.g., Bruce, 1982; Burton & Jenkins, 2011). Unlike unfamiliar faces, which have only been encountered on a few occasions, familiar faces activate stored representations in long-term

memory, which contain both visual and semantic information (such as biographical facts) about a person. If there are qualitative differences in the way in which familiar and unfamiliar faces are processed and encoded, one important difference might concern the role of attention for identity-specific processing. When encountering a familiar face, pre-existing perceptual memory representations of that person may be accessed with little or no attention, and these may be particularly hard to suppress. In contrast, the perception of unfamiliar face identity may require intentional processing for the formation and retention of an explicit memory trace. To address this question, Experiment 5 compared N250r amplitudes during two tasks: face identity matching (*explicit*) or target detection (*implicit*) on trials where two images showed either famous or non-famous individuals.

For unfamiliar faces, reliable temporal N250r repetition effects emerged, and these were strongly modulated by task demands: N250r responses were clearly present for the *explicit* but not for the *implicit* task (see Figure 6.4). This is exactly the pattern that was observed in Experiment 4, thus confirming that unfamiliar face recognition processes are strongly task-set dependent and thus not fully mandatory. Moreover, this was the case regardless of face format, as computer-generated faces were used in Experiment 4, while naturalistic faces were used in Experiment 5. The critical question was whether N250r responses would be elicited to famous face repetitions during implicit target detection. If famous face identity is processed in a fully mandatory fashion, an N250r should be elicited during the implicit task, reflecting immediate and automatic access to robust memory representations for familiar faces. However, results did not provide evidence for mandatory identity-related processing of famous faces (i.e., celebrities) with which observers were highly familiar.

For famous faces, an N250r was again only present for the explicit but was completely absent for the implicit task (see Figure 6.5), suggesting very similar effects of attention on identity-related processing, irrespective of whether or not face stimuli are familiar. Results thus demonstrate that familiarity with a face does not modulate the influence of strategic task-specific influences on identity-related processing during early stages of face perception and visual face memory. This suggests that the formation and retention of perceptual representations of individual faces requires identity-specific processing, regardless of whether or not pre-existing memory representations are available.

The observation that famous face recognition processes in Experiment 5 did not operate strictly mandatory, but were fully task-set dependent appears to contradict previous findings

of the presence of an N250r to famous face repetitions irrespective of their task relevance (e.g., Neumann & Schweinberger, 2008, 2009; Trenner et al., 2004). In particular, Trenner et al. (2004) used a similar paradigm to compare N250r repetition effects to famous faces during direct and indirect tasks; identity-matching (*direct*) or semantic classification of the second face in a pair as either singer or actor (*indirect*). Clear task differences were seen for N250r responses, which were significantly larger for the direct relative to the indirect task. However, the indirect task in this study required access to semantic information (i.e., person knowledge) that initially requires recognition of a person's identity. In contrast, *implicit* target detection in Experiment 5 did not require decisions based on semantic information about faces, but the detection of visual changes in the structure of a face stimulus (i.e., inversion).

The present findings raise the question whether observers were fully unaware of the presence of a famous person on some trials in the *implicit* task. The absence of N250r repetition effects to famous faces suggests that the identity of a previously seen familiar face was not mandatorily encoded and retained as a face memory trace, irrespective of its rich long-term memory representation. Nevertheless, observers reported after the experiment to have recognized some images of famous celebrities while searching for inverted face targets. One possibility is that this reported feeling of familiarity may reflect immediate and thus automatic access of 'person knowledge' (i.e., semantic information about a face such as the name of a famous actor, or a recent film in which he played). This would indicate that while the formation and retention of visual memory traces for individual faces requires intentional processing, post-perceptual face processes might operate largely in an obligatory fashion. This would imply that early (but not late) face processing stages including face perception and visual memory appear to be strongly modulated by task-specific influences, irrespective of whether or not faces are familiar. In contrast, access to semantic representations of a known person might be activated in a task-independent and thus obligatory manner, when face stimuli are familiar. This will need to be further clarified in future research.

Previous research has shown that the repetition-related N250r is typically larger for familiar than unfamiliar faces (e.g., Begleiter et al., 1995; Schweinberger et al., 1995). This enhancement in the N250r response to highly familiar faces has been linked to the instantaneous activation of pre-established perceptual memory representations for known faces. In contrast, an N250r of similar size emerged in Experiment 5 to repetitions of famous and non-famous faces in the *explicit* face identity-matching task. It is unclear why N250r

responses in the present study were not differentially modulated by visual familiarity with some of the face stimuli. One possible interpretation may be that different face processing mechanisms are engaged during tasks requiring same/different identity judgments relative to famous/non-famous decisions. The former requires a physical match between two face stimuli on the basis of identity-related facial cues, while the latter involves explicit access to stored representations of known faces in visual and/or semantic memory. Therefore, the fact that identity and not familiarity was the task-relevant attribute in the *explicit* task might have resulted in the activation of perceptual short-term memory processes relative to neural representations in long-term face memory that need to be accessed for familiarity judgments.

In summary, the aim of Experiment 5 was to find out whether familiarity affects the observed task-dependence of identity-related face processing. Findings demonstrated strong strategic task-specific influences on identity recognition, irrespective of whether face images showed famous celebrities or non-famous individuals. In other words, visual familiarity with a face and the availability of pre-existing visual face memory traces of familiar people did not facilitate the processing of identity-related facial cues in a face identity matching task. This suggests that similar perceptual mechanisms underlie familiar and unfamiliar face recognition, which show a considerable degree of task-set dependent (and thus not fully automatic) processing during early perceptual processing stages.

6.2.5 General Discussion. Experiments 4 and 5

Experiments 4 and 5 investigated the effects of visual attention and/or task relevance on identity-related face processing. N250r amplitudes were compared during two tasks: face identity matching (*explicit*) and target detection task (*implicit).* Unfamiliar face stimuli were used in Experiment 4, whereas face stimuli could either be images of famous celebrities or non-famous individuals in Experiment 5. The main research aim was to test whether repetition-related N250r components would be modulated by task demands, thus indicating either optional or obligatory neural processes for identity recognition. Results of Experiment 4 were clear-cut: Reliable N250r components to same face repetitions emerged for the explicit but not for the implicit task, indicating a strong impact of strategic processing on the perception of unfamiliar face identity. One important difference between implicit and explicit tasks relates to the need to encode and retain an active perceptual memory trace during explicit face identity matching, while there is no memory involvement during implicit target

detection. The absence of N250r repetition effects in a task that did not require the formation and retention of a visual memory representation of a previously seen face suggests that the underlying neural mechanisms are optional, effortful and strongly rely on attentional mechanisms.

An important difference between familiar and unfamiliar face perception lies in the way in which these two types of stimuli are processed and represented in visual memory (e.g., Burton & Jenkins, 2011). While unfamiliar face memories are largely based on information that is specific to a particular face image (*pictorial* codes) and are relatively transient (e.g., Pfütze et al., 2002), familiar faces activate strong memory traces in long-term memory. To test whether familiarity with a face would modulate the influence of strategic task-specific processing on identity recognition, images of famous celebrities were included in Experiment 5, for which rich perceptual face memories have been formed over time. Are stored perceptual face memories of famous individuals activated instantaneously and irrespective of task demands, thereby facilitating the formation and retention of an explicit memory trace of a familiar person in visual working memory?

The findings from Experiment 5 showed that despite their familiarity, repeated presentations of the same famous person did not elicit N250r components in the *implicit* task whereas reliable N250r responses were present to famous face repetitions in the *explicit* task. Thus, a strong task dependence of identity-related processing was found regardless of whether or not face stimuli were highly familiar. This suggests that the availability of rich perceptual images of a well-known famous face does not facilitate the activation of a memory trace of that person in visual short-term memory. In other words, there was no processing advantage during early stages of face perception and visual face memory for highly familiar faces. Therefore, despite behavioural evidence suggesting a functional distinction between familiar and unfamiliar face processing (e.g., Hancock et al., 2000), the present findings do not suggest that these two types of stimuli differ in their relative dependence or independence from attention and/or task demands during early perceptual processing. This is consistent with findings from neuroimaging studies, which suggest that neural systems for familiar as compared to unfamiliar face processing are very similar and thus not fundamentally different from one another (see Natu & O'Toole, 2011). This suggests that the same neural mechanisms underlie the perception of both familiar and unfamiliar faces, and that the

observed behavioural differences between these two types of faces may be largely quantitative rather than qualitative.

The novel finding of Experiments 4 and 5 is that identity-specific processing was fully optional in a task requiring the search for inverted face targets (*implicit*), and this was the case for both famous and non-famous faces. Thus, the present results do not support the idea that face identification is fully automatic and that specialized perceptual systems or 'modules' in the human brain, one of which dedicated to faces, operate fully mandatory. Instead, the current findings suggest that individual face recognition is neither fully mandatory nor completely task-set dependent. Moreover, whether or not visual face memories are formed seems to depend on an interplay of various factors related to the particular paradigm used, such as the nature and the particular instructions of the experimental task. In particular, the task-dependent involvement of visual face memory seems to play a critical role, as identity recognition was found to be mandatory in a view-matching task (Experiment 3), but optional and task-independent in *implicit* tasks that did not have this memory component (Experiments 4 and 5).

Despite the observation that identity-related processing of familiar faces requires attention in the same way as the processing of unfamiliar faces, this finding only relates to early stages of face perception and visual memory. However, visual familiarity is only one aspect of how we recognize familiar individuals, and person knowledge and emotional responses also play a key role in the successful identification of someone we know (Gobbini & Haxby, 2007). Neuroimaging evidence has shown that viewing someone familiar is associated with the instantaneous retrieval of 'person knowledge' about that individual, as reflected by neural activation in extended regions of the human face recognition system (Gobbini, Leibenluft, Santiago, & Haxby, 2004). In terms of Bruce and Young's (1986) model, visual recognition (mediated by face recognition units, or FRUs) precedes the access to person knowledge (mediated by person identity nodes, or PINs), and it is during those later post-perceptual stages that familiarity may strongly modulate the need of individual face recognition processes for attention. Thus, while the current findings suggest that perceptual face processing stages are not fully mandatory even for highly familiar faces, later semantic processing stages where name and biographic information of a famous person are retrieved may well be.

In conclusion, the present ERP results demonstrate that the processing of individual identity is strongly modulated by task-dependent attention and that these effects can be observed within 200 to 260 ms after stimulus repetition. Findings further highlight strong effects of strategic task-specific influences on identity-related processing irrespective of familiarity with a face. Moreover, the need to encode a visual face memory trace seems to be a critical determinant of whether identity recognition is optional or obligatory (see Experiment 3). Therefore, rather than reflecting absolute dependence on or independence from attention, the degree to which identity-related processing relies on task demands and/or attentional strategies is likely to be influenced by an interplay of different task parameters.

Chapter 7. Durability and decay of visual working memory (WM) for faces

One novelty of the research described so far is the use of rapid repetition paradigms where two face stimuli are presented at very brief stimulus onset asynchronies (SOA). These are long enough to prevent the formation of an iconic memory trace, yet much shorter than the SOA employed in previous face repetition studies (e.g., Schweinberger et al., 1995, 2004). Past research has shown that temporal parameters modulate face repetition effects by demonstrating that the length of the repetition interval affects the strength of the memory trace acquired to the first presentation of a stimulus (e.g., Henson, Rylands, Ross, Vuilleumier, & Rugg, 2004). This suggests that memory decay and/or interference by intervening items determine the durability of perceptual face representations in visual working memory (WM). Existing ERP studies have used a variety of different temporal parameters for stimulus presentation. For example, ISIs of ~1 second have repeatedly been used by Schweinberger et al. (2002, 2004), where reliable N250r repetition effects emerged to repetitions of famous faces. This suggests that newly acquired visual face memory traces are sustained during delayed interstimulus intervals when repetitions are immediate (i.e., without other faces intervening between repetitions; see also Itier & Taylor, 2004, for repetitions effects for unfamiliar faces). Moreover, familiarity with a face has been shown to modulate the robustness of visual face memories: While the N250r is eliminated by backward masking (Dörr et al., 2011) or by other faces intervening between face repetitions (Pfütze et al., 2002), this only applies to unfamiliar but not familiar faces. Thus, familiarity with a face influences the robustness of newly formed face representations over time, presumably due to facilitated maintenance via pre-established long-term face memories.

While Experiments 1-5 provided strong support for the rapid acquisition of view-independent perceptual face memories, the question arises whether these memory traces persist across longer interstimulus intervals (ISIs). To address this question, Experiment 6 presented pairs of unfamiliar faces with varying time lags between repetitions. On each trial, two face stimuli were presented for 200 ms each, and separated by either a 200 ms interval *(short*) or a 1200 ms ISI (*long*).

7.1 Experiment 6. Effects of repetition lag on WM for newly learned faces

7.1.1 Introduction

Memory has the ability to encode, store and recall information. When processing a visual stimulus, perceptual information is encoded and converted into a neural representation (i.e., a mental picture) for subsequent storage in memory. The processes that allow us to maintain and activate representations of incoming information that are immediately available for recall and/or further processing are referred to as working memory (WM), and can be thought of as an immediate or short-term storage of information prior to its transfer into long-term memory (Baddeley, 1992). In repetition priming tasks, visual information about the first stimulus is stored over brief periods of time in visual WM so that it can be immediately re-activated when the same or a related stimulus is repeated. With longer time intervals between encoding and recall, new memory traces are either converted into more stable representations in long-term memory, or fade away over time.

Several neuroimaging studies have investigated the neural basis of visual memory for faces (e.g., Ishai & Yago, 2006; Haxby et al., 2000). These suggest that a widely distributed cortical network mediates visual face memory, including temporal regions (i.e., fusiform gyrus), as well as parietal and frontal regions. Encoding and retrieval are likely to represent dissociable forms of memory with the former being associated with a more ventral system including left prefrontal cortices, whereas the latter activates a more dorsal system including right prefrontal and parietal areas (e.g., Bernstein, Beig, Siegenthaler, & Grady, 2002). In particular, the hippocampus in the medial temporal lobe appears to be primarily involved in various memory-related processes, including retention in short-term (or WM) and long-term memory. Within all regions associated with visual face memory including the FFA, correctly recognized previously seen faces evoked stronger activation than novel faces, indicating that familiarity with a face modulates the strength of the neural response during memory recall (Ishai & Yago, 2006). These findings further suggest that regions such as the FFA subserve different functions, which not only include the perception of individual identity, but also the maintenance of that information in face memory (see Druzgal & D'Esposito, 2001).

An important factor contributing to recognition memory is the degree to which new information is processed and/or incorporated into existing knowledge. Deeper levels of processing that involve a degree of abstract or semantic analysis yield more robust memory

traces, and are as a result remembered better (Craik & Tulving, 1975). Such effects have also been observed for faces (e.g., Bower & Karlin, 1974). This is further supported by fMRI evidence, demonstrating differential effects of encoding strategy on brain regions associated with memory for faces (Bernstein et al., 2002). In this study, unfamiliar faces were either intentionally learned or incidentally processed during identity-unrelated tasks. Each condition was followed by an explicit face memory test, where novel faces were intermixed with previously seen faces. Neural activity in fusiform gyrus was modulated by encoding strategy, suggesting that this region does not reflect purely automatic face processing, but is modulated by task-dependent attention.

Effects of repetition lag on face recognition memory

Various methods and techniques have been used in the past few years to study effects of stimulus repetitions using different repetition lags between initial and repeated presentation. Differences in repetition lag have been shown to affect memory-related face processes. Others (e.g., Henson et al., 2000) showed that neural activity to successive presentations of unfamiliar faces was modulated by the lag between first and second presentation of the same face where 1 and 147 stimuli (median of 45) intervened between repetitions, corresponding to time intervals of 8 seconds to 20 minutes. Neural responses to repeated unfamiliar faces decreased with lag, suggesting that repetition effects reflect visual WM processes that decay over brief periods of time. This lag sensitivity of face repetition effects further suggests that the underlying neural changes are temporary unless consolidated by further repetitions. These findings suggest that newly formed memory traces decay with time, unless new information is actively rehearsed. Further support for lag-related neural response modulations in distinct fusiform face regions comes from Fang et al. (2007). This study showed that for long lags, the size of the neural response was dependent on the degree of face rotation, while no such effect was found for short lags. However, it has been argued that these effects may mainly reflect quantitative rather than qualitative differences in neural processing (Henson et al., 2004). Furthermore, due to the varied nature of repetition lags in previous face research, differences in neural response properties may be partly attributable to varying time intervals between repeated stimulus presentations.

While it has been shown that increasing the time interval between encoding and recall modulates the strength of visual memory traces, another important factor for recognition

performance is WM load. ERP research has shown that N250r responses to famous face repetitions are independent of perceptual load at encoding when task-irrelevant unfamiliar faces compete with non-face objects for WM resources (Neumann & Schweinberger, 2008, 2009). This suggests that the identity of familiar faces is to a considerable degree processed in an automatic fashion, irrespective of perceptual load. However, when famous faces served as distractor stimuli, face repetition effects were reduced or even eliminated under high load, suggesting that, at least under high demands, task-irrelevant face processing may be limited to one face at a time. Others (e.g., Morgan, Klein, Boehm, Shapiro, & Linden, 2008) have shown that WM memory load also modulates unfamiliar face recognition processes. In this study, participants viewed face arrays that included between one and four unfamiliar faces during encoding followed by a single test face at recall. Participants' task was to indicate whether or not the target face matched one of the faces in the encoding array. N250r responses were significantly reduced for higher memory loads (i.e., three or four faces present at encoding), suggesting that facilitated processing of repeated faces is weaker under limited WM resources. Enhanced visual short-term memory has also been shown for emotional faces, as reflected by increased N250r amplitudes to emotional relative to neutral faces, and this emotional enhancement has been attributed to improved maintenance and/or retrieval of emotional stimuli (Langeslag, Morgan, Jackson, Linden, & Van Strien, 2009).

The robustness of perceptual face memories in WM

Individual face recognition requires memory representations of invariant aspects of faces across image variability. How long lasting are identity-specific structural codes that are derived from a familiar face? It appears plausible to assume that visual WM representations of novel stimuli gradually fade away over a short period of time, unless perceptual information is actively maintained. At present, it is still an on-going debate whether memory traces simply decay due to the mere passage of time ('decay theory'; Conrad & Hille, 1958). According to this view, information is less available for later retrieval as time passes and memory, as well as memory strength, wears away. Findings from Experiments 1-6 have shown that perceptual face memories to rapidly presented individual faces are reliably obtained across *pictorial* changes (i.e., view), indicating that those representations are based on the analysis of identity-specific *structural* codes (see Bruce & Young, 1986). However, little is known about the durability of structural WM representations of unfamiliar faces over

longer time intervals between repetitions. Do longer repetition lags not only modulate the strength of a perceptual face memory trace, but also differentially affect the maintenance of different types of visual codes in memory? In other words, is it more difficult to store a high-level structural relative to a low-level pictorial face memory trace over longer periods of time?

Evidence from face adaptation paradigms has shown that structural representations of altered images of famous faces are not only immediately stored but that these memory traces are also long-lasting. Carbon et al. (2007) presented participants with configurally altered images of famous faces during an adaptation phase. These images were created by changing the distance between the eyes and the mouth. After a delay of either 5min or 24h, participants were asked to identity the original famous face image from a series of images. Results showed that participants' decisions were biased toward previously seen distorted images of a famous person, suggesting that prior exposure to an altered face image had biased later performance on a recognition memory test. Importantly, such adaptation effects were not only found when identical images sharing the same visual features were used, but also for different images, suggesting that identity-specific information about faces had been extracted. Moreover, the finding that adaptation effects were weaker but still reliable after a 24h delay compared with those effects obtained after 5min suggests that time lag had similar effects on newly formed representations of famous faces regardless of whether those were based on pictorial or structural codes. However, Carbon et al., investigated mechanisms of long-term memory for highly familiar faces and it is unclear whether similar neural processes underlie short-term and/or WM storage of unfamiliar faces.

Research aims

Experiment 6 investigated whether newly acquired perceptual face memories represent fast-decaying WM representations, and whether the strength of these memory traces is modulated by the type of encoded facial information (i.e., *pictorial* view-dependent versus *structural* view-independent). Two faces were presented at *short* or *long* ISIs (200 ms versus 1200 ms), showing either the same or two different individuals, in either the same or two different views. Participants performed a view-matching task where identity is task-irrelevant but nevertheless encoded in an obligatory fashion (see Experiment 3). If increasing the time interval between repeated presentations of the same individual face modulates the strength

of the face memory representation acquired to the first presentation, N250r responses should be attenuated or even abolished on trials with *long* ISIs. Moreover, if it is more difficult to maintain a high-level structural than a low-level pictorial face representation in WM, N250r components should become more strongly view-dependent when the time interval between repetitions of the same face increases.

7.1.2 Method

Participants

Twelve paid volunteers (nine females), aged 25 to 37 years (mean age 30 years, SD = 4) were tested. Data from two further participants was excluded due to an insufficient number of artifact-free EEG trials (less than 60% of all trials left after artifact rejection). All participants were right-handed, had normal or corrected-to-normal vision, and gave written informed consent prior to testing.

Stimuli and procedure

These were identical to Experiment 3 in all respects, except that two face images were either presented with *short* or *long* interstimulus intervals (ISIs of 200 ms or 1200 ms). Face stimuli were greyscale images of 30 naturalistic faces (15 female) shown in two views, a full front view and a right-tilted side view (i.e., at an angle of approximately 45°). Figure 7.1 (bottom panel) illustrates face stimulus sequences on each trial. Two faces showed either the same or two different individuals, in either the same (front-front or side-side) or two different views (front-side or side-front). Temporal parameters for *short* and *long* ISIs employed in the present study are shown in Figure 7.1 (top panel). For *short* ISIs, two faces were presented for 200 ms each, separated by a 200 ms ISI. For *long* ISIs, two faces in a pair were shown for 200 ms each, separated by a 1200 ms ISI. On those trials, a fixation cross appeared 500 ms prior to the onset of the first stimulus in a pair and disappeared when this stimulus was presented. Eight consecutive blocks were run for each ISI. Six participants started with the long ISI condition first, while the remaining six performed the short ISI condition first. Eighty trials per block (20 trials for each combination of identity and view) were run for blocks with *short* ISIs. Fifty-six trials per block (7 trials for each combination of identity and view) were run for blocks with *long* ISIs to ensure similar block length across ISIs. The experiment lasted approximately 25 min, and participants performed two training blocks (one for each ISI) prior to the experiment.

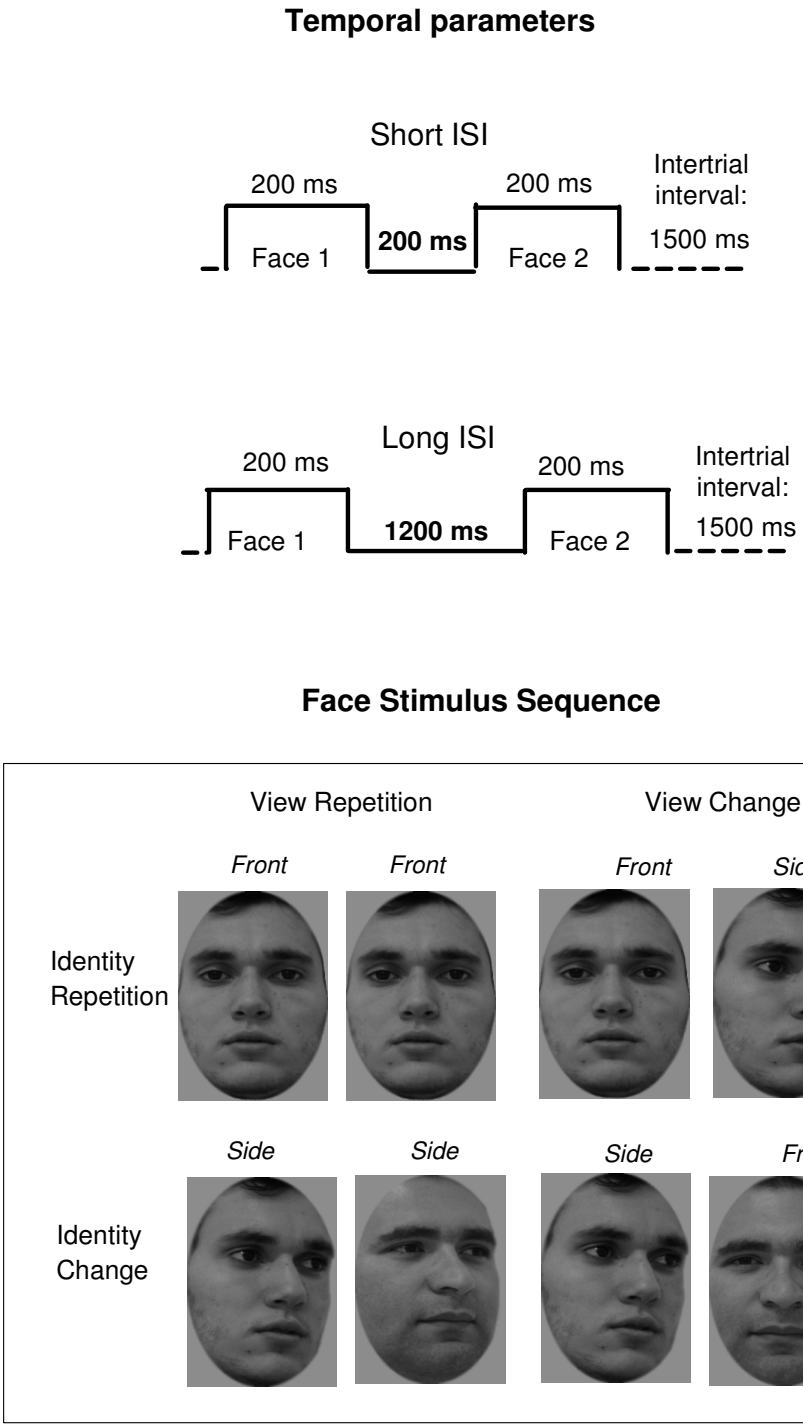


Figure 7.1 Top panel: Temporal parameters of stimulus presentation on each trial for *short* and *long* ISIs. Bottom panel: Examples of the four different face stimulus sequences. On each trial, two faces showed either the same or two different identities (identity-repetition versus identity-change), in either the same view (front-front or side-side; view repetition) or two different views (front-side or side-front; view change). Note that the second image was always 20% larger than the first image.

EEG recording and data analysis

These were identical to Experiment 3, except that analyses included the additional factor ISI (*long* versus *short*). Mean amplitude values were computed at posterior electrodes P9/10 for the N170 time window (160-190 ms after the onset of the second face) and for early and late N250r time windows (210-260 ms or 260-310 ms after the onset of the second face). Repeated-measures analyses of variance (ANOVAs) were performed for factors identity (identity-repetition versus identity-change), view (view-repetition versus view-change), and ISI (long versus short). Analogous analyses were also conducted at frontal electrode Fz.

7.1.3 Results

Behaviour

Overall accuracy for the view-matching task was 94%. Participants were more accurate for identity-repetition than identity-change trials (95% versus 93%; $F(1,11) = 34.8$; $p < .001$), but there was no reliable main effect of view ($F < 1$). A main effect of ISI approached significance ($F(1,11) = 4.6$; $p < .06$), suggesting that accuracy was higher for *short* relative to *long* ISIs (95% versus 93%). An identity x view interaction demonstrated that accuracy was significantly higher on identity-repetition trials where two faces showed the same relative to two different views (96% versus 94%; $F(1,11) = 10.1$; $p < .01$), whereas no such effect was found for identity-change trials. There were no interactions between identity and ISI ($F(1,11) = 1.1$; $p = .29$), and no three-way interaction (identity x view x ISI: $F < 1$).

Mean RT was 567 ms. There were significant main effects of identity ($F(1,11) = 54.3$; $p < .001$) and view ($F(1,11) = 6.8$; $p < .03$), indicating faster RTs for repetitions as compared to changes of identity (558 ms versus 576 ms), as well as for repetitions versus changes of view (556 ms versus 579 ms). RTs were faster for short versus long ISIs (542 ms versus 592 ms) but this effect was not reliable ($F(1,11) = 3.8$; $p < .08$). An interaction between identity and view ($F(1,11) = 49.6$; $p < .001$) demonstrated faster responses on trials where neither identity nor view changed than on trials where view differed (535 ms versus 582 ms), but there was no difference in RTs on trials where only identity or both attributes differed (577 ms and 576 ms, respectively). A significant identity x ISI interaction ($F(1,11) = 5.2$; $p < .05$) showed that RTs were faster for identity-repetitions for short versus long ISIs (528 ms versus 588 ms), whereas no such effect was present for identity-change trials. There was no reliable three-way interaction (identity x view x ISI: $F(1,11) = 3.8$; $p < .08$).

ERP markers of visual face memory

Figure 7.2 shows grand averaged ERP waveforms obtained at posterior electrode pair P9/10 and anterior electrode Fz in the 400 ms interval for identity-repetition and identity-change trials, collapsed across view repetitions and view changes. ERPs are shown separately for *short* ISIs (top panel) and *long* ISIs (bottom panel). N250r components were clearly present for both ISIs, but these were markedly smaller when two faces of the same individual were repeated with long ISIs. Moreover, N250r onset latencies were delayed by ~ 50 ms for trials with long ISIs. Therefore ERP data were analysed separately for *early* and *late* N250r time windows (210-260 ms and 260-310 ms, respectively). Figure 7.3 illustrates topographic N250r scalp maps showing characteristic enhanced posterior negativities over occipito-temporal regions accompanied by a frontal positivity, separately for short and long ISIs, and for the early and late N250r time windows. On trials with short ISIs, an N250r reliably emerged in the early 210-260 ms time window, where it was absent on trials with long ISIs. In the late 260-310 ms time window, an N250r emerged for both ISIs, although this component was attenuated for long relative to short ISIs. ERPs were also averaged for view-repetition and view-change trials, separately for short ISIs (top panel) and long ISIs (bottom panel), as shown in Figure 7.4. Even though the N250r was strongly reduced on trials with a long ISI, similar N250r components were present on trials with either a repetition or a change of view for both short and long ISIs.

Analyses in the 160-190 ms time interval showed no main effect of identity on the early face-selective N170 component ($F < 1$).

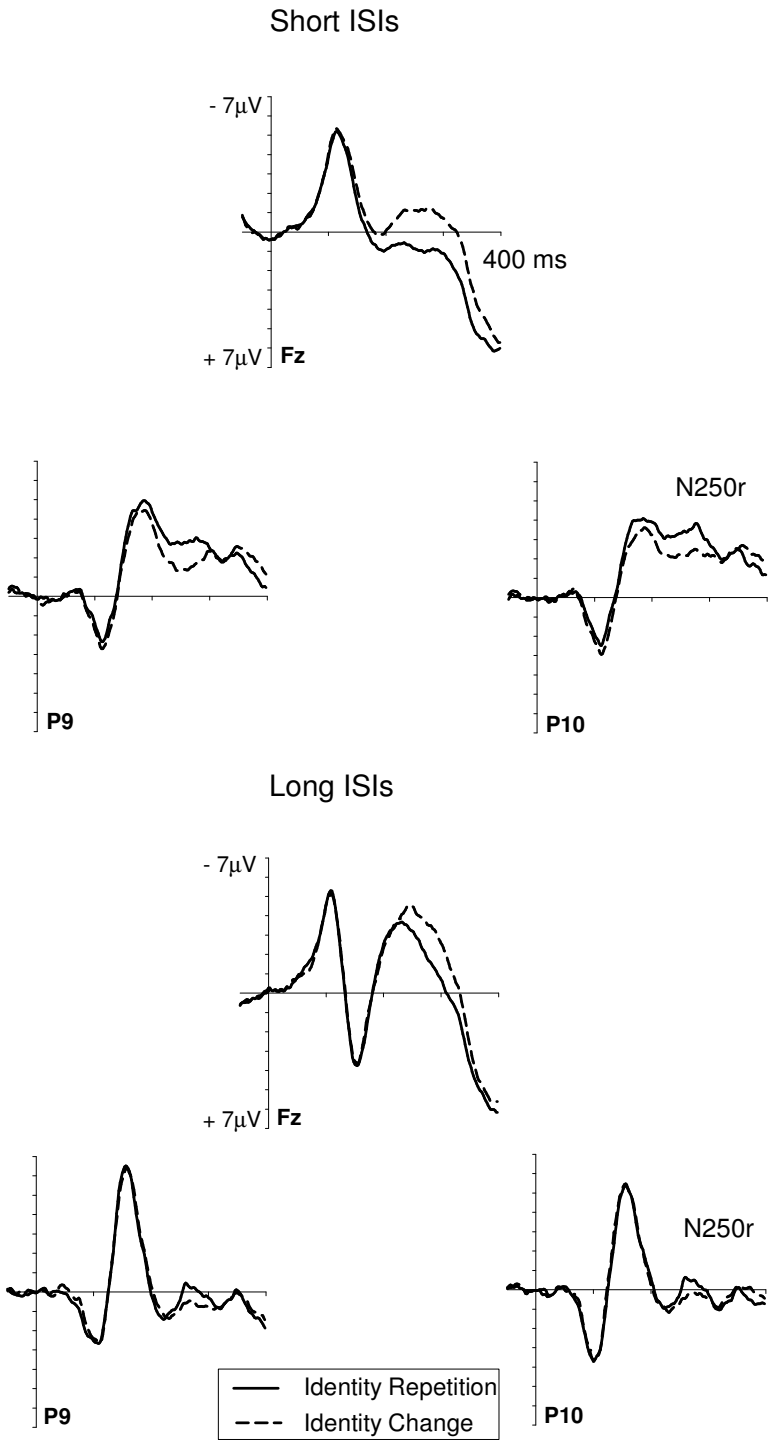


Figure 7.2 Grand averaged ERP waveforms obtained at lateral posterior electrode pair P9/10 and frontal anterior electrode Fz in the 400 ms interval after the onset of the second stimulus in a face pair for identity-repetition (solid lines) and identity-change trials (dashed lines). ERP data are shown separately for *short* ISIs (top panels) and *long* ISIs (bottom panels), but are collapsed across view-repetition and view-change trials.

Early time window (210-260ms). Reliable N250r components emerged at posterior temporal electrode pair P9/10 in the early 210-260 ms time window ($F(1,11) = 9.3$; $p < .02$). There was no interaction between identity and view ($F < 1$), but a significant interaction between identity and ISI ($F(1,11) = 13.1$; $p < .01$), as well as a three-way interaction (identity x view x ISI: $F(1,11) = 6.0$; $p < .04$). Separate follow-up analyses were performed for each ISI. For *short* ISIs, the presence of an N250r component in the early 210-260 ms time window ($F(1,11) = 14.8$; $p < .01$) confirmed previous findings of an early onset of the N250r for rapid repetitions of the same individual face. An identity x view interaction approached significance ($F(1,11) = 4.8$; $p < .06$), indicating that the N250r tended to be larger for view-repetition as compared to view-change trials**.** Follow-up analyses showed that an N250r was elicited on both view-repetition ($F(1,11) = 14.5$; $p < .01$) and view-change trials ($F(1,11) = 7.5$; $p < .02$). A different picture emerged for *long* ISIs: Here, an N250r was absent in the early time window ($F(1,11) = 1.1$; $p = .322$), and there was no identity x view interaction ($F < 1$).

The anterior N250r was accompanied by a frontal positivity at anterior midline electrode Fz in the early 210-260 ms time window ($F(1,11) = 7.2$; $p < .03$). A two-way identity x ISI interaction was significant ($F(1,11) = 5$; $p < .05$), and an interaction between identity and view approached significance ($F(1,11) = 4.5$; $p < .06$). There was also a three-way interaction (identity x view x ISI: $F(1,11) = 6.9$; $p < .03$). Separate analyses were conducted for each ISI. For *short* ISIs, there was a main effect of identity ($F(1,11) = 9.6$; $p < .02$), and a significant interaction between identity and view ($F(1,11) = 11.5$; $p < .01$). Follow-up one-tailed t-tests confirmed that an anterior N250r was clearly triggered on view-repetition trials ($t(11) = 3.5$; $p < .01$), but was absent on view-change trials ($t(11) = 1.7$; $p = .122$). Similar to the posterior N250r, a main effect of identity was absent on trials with *long* ISIs ($F(1,11) = 2.1$; $p = .177$), and there was no identity x view interaction ($F < 1$), demonstrating the delayed onset of the N250r with longer time lags between repetitions.

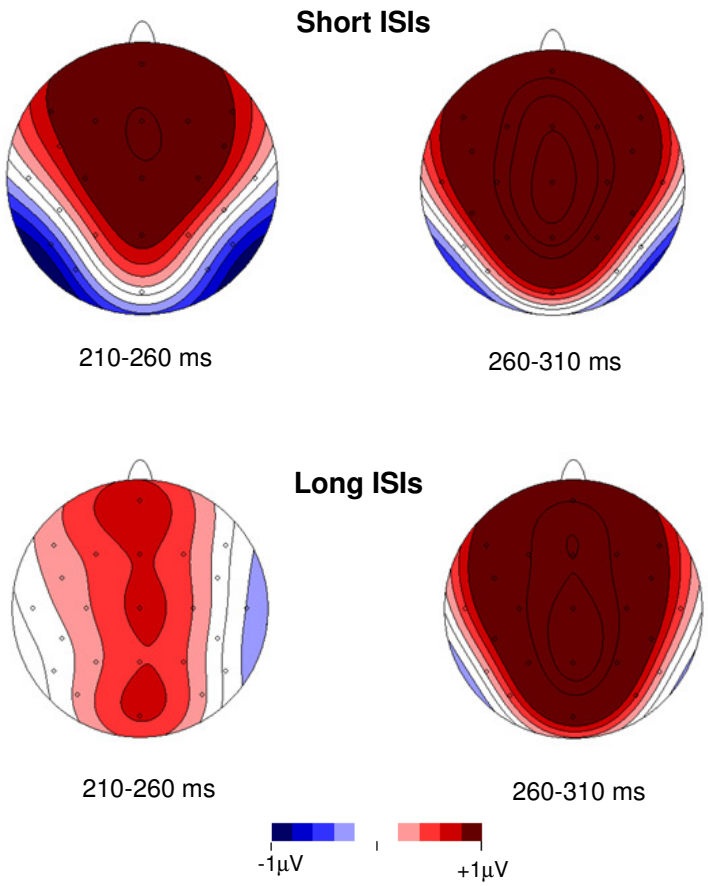


Figure 7.3 Topographic maps of N250r difference waves obtained by subtracting ERPs on identity-change trials from ERPs on identity-repetition trials, shown separately for *short* and *long* ISIs, and for the *early* and *late* N250r time windows (210-260 ms and 260-310 ms, respectively).

Late time window (260-310 ms). A late posterior N250r emerged in the 260-310 ms time window ($F(1,11) = 7.5$; $p < .03$), and was accompanied by a significant three-way interaction (identity x view x ISI: $F(1,11) = 7.7$; $p < .02$). There were no reliable interactions between identity and view ($F < 1$), or between identity and ISI ($F(1,11) = 2.2$; $p = .165$). Separate follow-up analyses confirmed the presence of an N250r for both *short* ISIs ($F(1,11) = 7.2$; $p < .03$) and *long* ISIs ($F(1,11) = 5.7$; $p < .04$) during this late time window. As can be seen in Figure 7.4 (top panel), N250r components elicited on trials with *short* ISIs were more sustained on view-repetition than on view-change trials, and an identity x view interaction approached significance ($F(1,11) = 4.8$; $p < .06$). Follow-up analyses confirmed that an N250r was no longer present for *short* ISIs on view-repetition trials in the late 260-310 ms time interval ($F(1,11) = 3.0$; $p = .110$), where it was still present on view-change trials ($F(1,11) = 12.9$; $p < .01$). In

contrast, for l*ong* ISIs an identity x view interaction was absent in the late 260-310 ms time window ($F < 1$), indicating a delayed onset of the N250r on those types of trials regardless of view (repetition or change).

A late anterior N250r was also present in the 260-310 ms time window ($F(1,11) = 10.1$; $p < .01$), and was accompanied by an interaction between identity and view ($F(1,11) = 16.4$; $p < .01$), as well as a three-way interaction (identity x view x ISI: $F(1,11) = 5$; $p < .05$). There was no reliable interaction between identity and ISI ($F < 1$). Separate follow-up analyses were conducted for each ISI. These demonstrated the presence of anterior N250r on trials with both *short* ISIs ($F(1,11) = 10.6$; $p < .01$) and *long* ISIs ($F(1,11) = 7.3$; $p < .03$). Reliable identity x view interactions were obtained for both types of trials ($F(1,11) = 22.9$ and 5.1; $p < .01$ and $p < .05$, for *short* and *long* ISIs, respectively). One-tailed t-tests demonstrated the presence of an N250r on view-repetition trials for both types of ISI ($t(11) = 4.4$ and 2.9; both $p < .02$, for *shor*t versus *long* ISIs), and its absence on view-change trials ($t(11) = .74$ and 1.8; both $p > .11$, for *short* versus *long* ISIs).

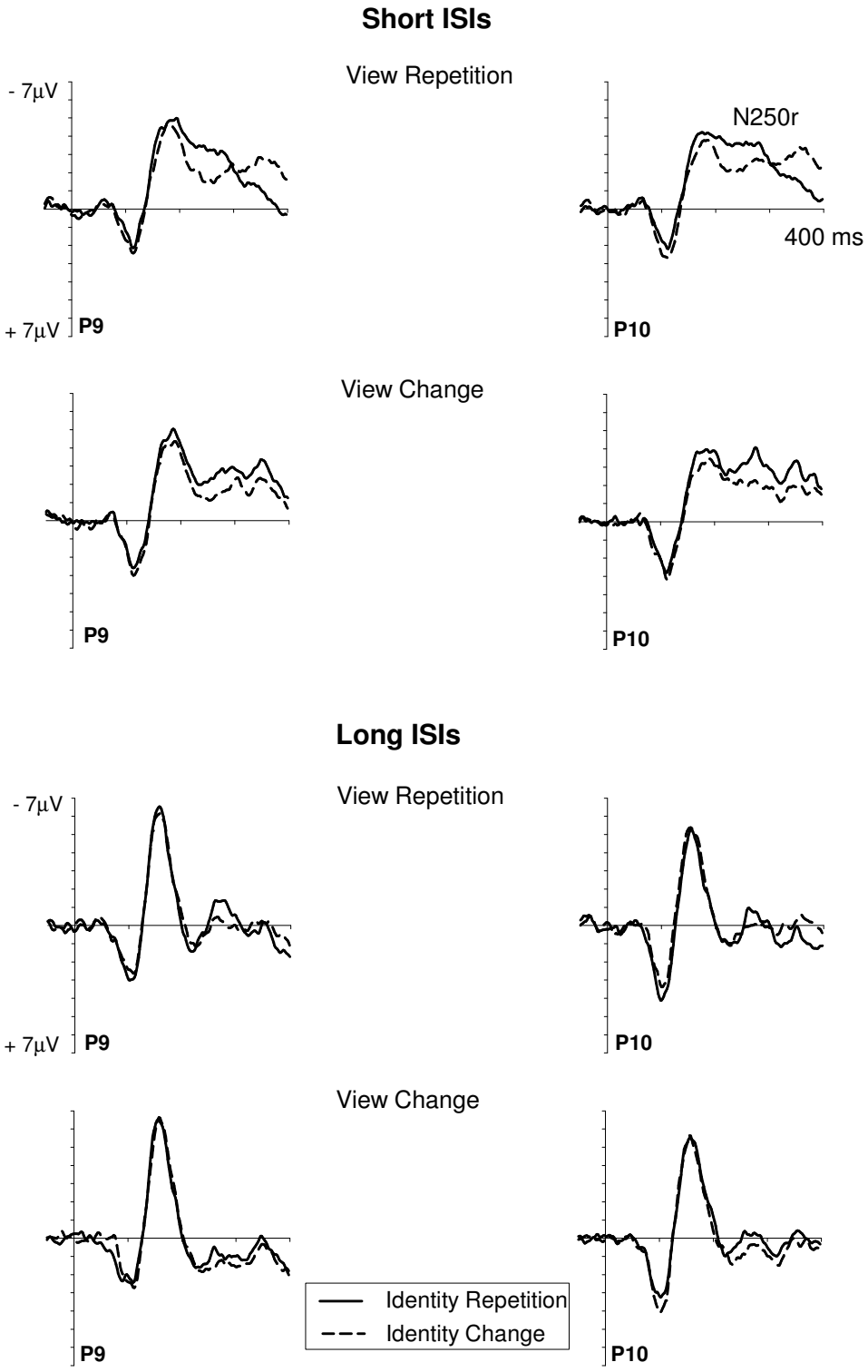


Figure 7.4 Grand averaged ERP waveforms obtained at posterior electrode pair P9/10 in the 400 ms interval after the onset of the second stimulus in a face pair for identity-repetition trials (solid lines) and identity-change trials (dashed lines), shown separately for *short* ISIs (top panels) and *long* ISIs (bottom panels), and for view-repetition and view-change trials.

7.1.4 Discussion

To investigate the effects of repetition lag on visual WM for faces, Experiment 6 presented pairs of unfamiliar faces with either *short* or *long* interstimulus intervals (200 ms or 1200 ms). Participants performed a view-matching task, and had to decide on each trial whether two faces showed the same or two different views, regardless of their identity. Two factors thought to influence the durability of visual WM representations were manipulated: the time interval between face repetitions, and the overlap of perceptual information between first and second presentation of the same individual face (*pictorial* or *structural*). It was hypothesized that if rapidly acquired visual face memories reflect transient neural representations that fade away within a few hundreds of milliseconds, N250r responses should be strongly modulated by the length of the repetition interval between face presentations. Moreover, if it is more difficult to maintain a structural than a pictorial face memory representation over time, this should be reflected by considerably smaller N250r amplitudes on view-change as compared to view-repetition trials under *long* ISI conditions.

Reliable N250r components emerged to repetitions of the same face in the *early* 210-260 ms time window on trials with *short* ISIs, replicating previous findings reported in earlier chapters of this thesis (Chapters 3-6) of fast encoding and activation of newly acquired perceptual representations to unfamiliar faces (see Figure 7.2, top panel). Again, these perceptual face memories were reliably triggered across view-repetition and view-change trials, demonstrating a considerable degree of view-independence. The main research aim of the present experiment was to assess the nature of perceptual face memories for longer repetition intervals, and to test whether the strength of these memory traces is modulated by the need to extract abstract view-independent relative to view-dependent facial cues. In repetition paradigms, information about the first stimulus needs to be extracted and stored within visual WM for immediate use when the same stimulus is repeated. If the interval between first and repeated presentation is longer, it should be more difficult to maintain an active memory trace of newly acquired visual information. This is exactly what was found on trials with *long* ISIs: Here, an N250r was absent in the 210-260 ms time window, but reliably emerged with a delayed onset of ~ 50 ms in the 260-310 ms time interval after the onset of the second face in a pair (see Figure 7.2, bottom panel). Moreover, N250r amplitudes were not only delayed but also noticeably smaller for *long* relative to *short* ISIs, which is thought to reflect weaker perceptual face representations with longer repetition lags. Importantly,

N250r responses on trials with long ISIs were very similar regardless of whether face-matching processes were based on high-level structural or low-level pictorial information. These findings not only demonstrate that long repetition intervals modulate the strength of visual WM representations of individual faces, but also suggest that this modulation is similar for structural and pictorial representations of individual faces. This suggests that WM representations of unfamiliar faces are based on identity-specific information and decrease in strength over time (see Carbon et al., 2007, for similar findings).

In the *late* 260-310 ms time window, N250r responses were still present for *short* ISIs but only on view-change trials, while this component was no longer present on view-repetition trials. This confirms previous findings of Experiment 2, demonstrating that N250r responses are more sustained on trials with a view change, presumably due to the difficulty to match unfamiliar faces on the basis of more abstract information about facial identity. Unlike the present study, Schweinberger et al. (2002) reported larger N250r amplitudes to repetitions of the same image relative to two different images of the same famous face, when successive presentations were separated by ~ 1 second interstimulus intervals (ISIs). This difference between a more sustained N250r for same face repetitions across different views in the current experiment, and an attenuated N250r for different-image repetitions found by Schweinberger et al. (2002) may relate to the importance of two critical parameters for WM representations: the initial memory strength of a stimulus, and the length of the repetition interval between first and repeated encounter. In Schweinberger et al.'s study, participants viewed the first face image for 1 sec, allowing ample time for a detailed and rich visual analysis of its unique facial features. In contrast, shorter exposure times of 200 ms to the first stimulus were used in the present study. Therefore, encoding time may not only modulate the initial memory strength but also the image-specificity of this memory trace.

The presence of a reliable N250r with longer repetition intervals highlights the efficiency of face-selective WM processes to successfully maintain individual face representations over brief periods of time, and further demonstrates that these representations are not based on purely perceptual but more abstract identity-specific codes. Moreover, the delayed onset of N250r components on trials with *long* ISIs emphasizes the flexible nature of face-selective perceptual mechanisms, which are speeded up with short retention intervals, but delayed with longer repetition lags, reflecting higher demands on WM maintenance and impeded access to stored face representations. The finding that N250r scalp topographies were very

similar across ISIs further suggests that the observed differences for short versus long ISIs are likely to be quantitative rather than qualitative (see Henson et al., 2004). Results suggest that increasing the temporal demands on WM affects the memory strength of individual face representations, regardless of the type of visual code on which these representations are based. Thus, different types of visually-derived codes from individual faces engage the same visual WM processes. The observation that perceptual face memory traces decrease in strength over short periods of time further suggests that forgetting occurs as a result of memory decay over time and that WM memory activations gradually weaken within several hundred milliseconds after a stimulus has disappeared from view. Thus, the duration for which visuo-perceptual information about faces needs to be maintained in memory appears to be an important determinant for successful face recognition.

As is clear from everyday experience, memories are often retrieved incidentally, without a prior intention to remember. Therefore, an interesting question concerns whether the same neural processes are engaged during intentional and incidental recognition of a previously encountered face. Past research has shown that the depth of visual processing influences how well information is remembered (e.g., Craik & Tulving, 1975), suggesting that there are differences in memory strength between intentional and incidental maintenance of new information. The present study employed a view-matching task, where identity-specific facial cues were task-irrelevant but were nevertheless extracted in an *implicit* and obligatory fashion (see Experiment 3). The observation that incidentally acquired visuo-perceptual face memories are maintained in WM memory across longer repetition intervals suggests that mandatory face processes underlie not only the encoding of identity-related information but also the maintenance and re-activation of this information in WM. However, as previously demonstrated (see Experiments 5 and 6), specific task demands such as the requirement to actively maintain a WM trace of a previously seen face are important factors mediating both the way in which individual faces are stored in visual memory, as well as the durability of these memory traces. Therefore, the nature and strength of memory representations of unfamiliar faces is likely to be mediated by an interplay of the passage of time (i.e., forgetting) and encoding strategy (i.e., the level of attentional control over what information from a face is processed).

Consistent with the current ERP findings, behavioural responses on the view-matching task were more accurate and faster for short relative to long ISIs, which are thought to reflect the

difficulty to maintain a face memory trace over longer repetition intervals. Thus, both ERP and behavioural measures demonstrate that unfamiliar face recognition processes are strongly modulated by increasing temporal demands on WM maintenance, but are not modulated by the nature of the underlying face representation. However, the present study only addressed mechanisms of visual short-term and/or WM, where view-independent face recognition processes emerged for repetition intervals in the time range of milliseconds to seconds. In contrast, in typical behavioural face recognition tasks, identity-related information has to be maintained over much longer time periods. It is therefore possible that structural face representations sustain short WM delays, but decay with longer retention intervals, where memory traces based on pictorial codes may still be available. Therefore, discrepancies between behavioural findings of largely pictorially based (i.e., view-dependent) unfamiliar face recognition and ERP findings of view-independent recognition might be attributable to differences in memory retention. To investigate this further, it would be interesting to test recognition memory for unfamiliar faces after a much longer retention interval (i.e., several minutes to days) to track the transition of newly formed WM representation of individual faces into long-term memory and to further clarify the nature of these memory traces.

In summary, Experiment 7 demonstrated that view-invariant face recognition processes sustain increased time intervals between initial and repeated face presentation, reflecting a degree of robustness of WM representations over short time periods and view changes. However, the finding that perceptual face memories were significantly weakened for longer repetition lags indicates the rapid decay of visual WM traces of individual faces over short periods of time. The finding of delayed N250r onset latencies for long ISIs is likely to reflect the difficulty to maintain and access perceptual face memories over time. Taken together, results demonstrate that visual WM representations of individual faces represent a fast-decaying store of facial information for both pictorial and structural face memories.

Chapter 8. Mechanisms of face perception and visual face memory in developmental prosopagnosia (DP)

The previous chapters have focused on the neural basis of face perception and face memory in adults with normally functioning face recognition abilities. However, important additional insights into face perception and its underlying mechanisms can be obtained by investigating the nature of severe face recognition impairments, as is the case in individuals with developmental prosopagnosia (DP). The present chapter outlines Experiment 7, which addresses the neural mechanisms that underlie face-selective recognition difficulties in DP. In contrast to acquired prosopagnosia, individuals with DP have no known history of neurological damage (e.g., Behrmann & Avidan, 2005; Duchaine & Nakayama, 2006). Their face recognition deficits are believed to be present from an early age, due to a failure to develop a fully functioning face recognition architecture (see Duchaine, 2011, for a review). Research suggests that developmental prosopagnosia is a heterogeneous disorder as reflected by different processing loci of impairment (Le Grand et al., 2006; Harris, Duchaine, & Nakayama, 2005). Two types of prosopagnosia have been distinguished for AP (De Renzi et al., 1991). Perceptual or apperceptive prosopagnosia is characterized by a disruption of early perceptual face processes whereas associative prosopagnosia is related to dysfunctional semantic processing stages.

Individual face recognition is a complex process where a series of distinct processing stages, including early perceptual and late post-perceptual stages, operate sequentially and relatively independently from one another. Successful face recognition relies on completion of each individual sub-stage (see Bruce & Young, 1986; Haxby et al., 2000). Even though individuals with DP are severely impaired in the explicit recognition of familiar faces, physiological and behavioural evidence suggest the existence of covert neural markers of familiarity. That is, despite an inability to explicitly recognize a face, behavioural responses distinguish systematically between familiar and unfamiliar faces. This is reflected by increases in skin conductance (Bauer, 1984) or above-chance performance in face-name matching tasks in response to familiar faces that are not consciously recognized (Young, Hellawell, & De Haan, 1988; Diamond, Valentine, Mayes, & Sandel, 1994). These covert responses indicate the presence of some kind of intact or spared face-selective neural mechanism in the absence of conscious face recognition in DP. At present, relatively few studies have investigated the

neural basis of implicit face recognition in developmental prosopagnosia (but see Eimer et al., 2012, for an exception). The aim of Experiment 7 was to address two related questions: First, do DPs process identity-related information about unfamiliar faces in a task context where facial identity is not relevant? Second, is an N250r elicited in the DP group on trials with a view change, requiring the extraction of abstract view-invariant information about face structure? To examine these questions, N250r components to unfamiliar face repetitions were directly compared for DP and control participants in a view-matching task where two faces either showed the same or two different views.

8.1 Experiment 7. Implicit face identity processing in DP

8.1.1 Introduction

The observation that face recognition is effortlessly achieved in typical adults contrasts markedly with the immense challenge it poses for individuals with DP. What is the underlying neural basis of this deficit and which processing stages are affected? In acquired prosopagnosia (AP), a distinction has been made between recognition impairments that either involve familiar or unfamiliar faces (see Tippett, Miller, & Farah, 2000), indicating a double dissociation between these two types of face recognition. Some individuals with AP perform normal when matching unfamiliar faces while the recognition of familiar faces is severely impaired (see Benton & Van Allen, 1972). Others show the exact opposite pattern: They are completely unable to learn new facial identities while recognition of familiar faces (e.g., faces known before the onset of AP) is preserved (Malone et al., 1982; Duchaine & Weidenfeld, 2003). The finding that familiar and unfamiliar face recognition processes can be selectively impaired in prosopagnosia is in line with the assumption that those two types of faces rely on distinct neural mechanisms (Hancock et al., 2000). In marked contrast to acquired cases, individuals with developmental prosopagnosia are assumed to have processing deficits that impair, among other things, the perceptual learning of faces (e.g., Duchaine & Nakayama, 2006). However, the exact locus of this impairment is less clear. If face processing impairments can selectively occur at post-perceptual processing stages, normal early perceptual face processes should be observable in some individuals with DPs. Such an interpretation is in line with the 'disconnection hypothesis' proposed by Burton et al. (1991), which assumes that face recognition deficits in some DPs arise due to disconnections between sub-components within an otherwise intact face processing system. From this

perspective, DP is, in some instances, caused by functionally impaired links between visual-perceptual face representations and higher order modality-independent representations of faces reflecting the final stages of face recognition. However, an alternative account proposed by Farah, O'Reilly, and Vecera (1993) argues that face recognition deficits always originate from impairments of early perceptual processes. According to this view, prosopagnosia is always characterized by some deficit during early face perception.

A degree of functional normality: The neural basis of DP

Research into the neural basis of prosopagnosia has provided inconclusive evidence, suggesting that selective deficits in processing distinct information from faces are associated with different loci of neurological impairments. While several studies demonstrated spared implicit or covert processing of familiarity in the absence of explicit face recognition in AP (e.g., Bauer, 1984; Young et al., 1988), less research has focused on covert face recognition in developmental cases (see Towler & Eimer, 2012, for a review). Behavioural evidence indicates the existence of covert markers of face recognition also in DP, which suggests that similar neural mechanisms underlie acquired and developmental types of prosopagnosia. Avidan and Behrmann (2008) tested six individuals with DP in a task that required same/different identity judgments of two sequentially presented faces that were either famous or non-famous. Recognition performance was better when famous faces were repeated, even though explicit recognition of those faces was markedly impaired, indicating implicit familiarity processing in DP. This finding is consistent with reports of above-chance performance in a group of eleven DPs during an explicit familiarity task requiring famous/non-famous judgments of two simultaneously presented faces, despite poor explicit face recognition (Rivolta, Palermo, Schmalzl, & Coltheart, 2012). However, Rivolta et al. did not find evidence for covert recognition of face-name associations in an implicit face-priming task. Overall, findings of covert neural markers of familiarity demonstrate that some face-selective neural mechanisms are intact in DP, indicating a degree of spared functional normality despite severe face recognition impairments. However, and in line with Farah et al. (1993), behavioural performance measures may not be ideally suited to clarify the exact nature and neural basis of covert face recognition. Therefore, the question arises whether the existence of implicit face familiarity processing in behavioural tests indicates typical underlying mechanisms at the cognitive or neural level?

Electrophysiological measures provide a superior tool to study the presence of covert face recognition processes and its underlying functional properties, because they can be obtained independently of behavioural performance. In a recent study, Eimer et al. (2012) measured event-related brain potentials (ERPs) in a group of twelve DPs during a task that required famous/ non-famous familiarity judgments. The research aim was to test whether neural markers of face recognition (N250 components) would be triggered by familiar faces in the absence of conscious recognition of those faces. This is exactly what was found in a sub-sample of six participants: Despite an inability to consciously recognize faces of celebrities, N250 responses clearly distinguished between non-recognized famous and non-famous faces. Moreover, the N250 component triggered by successfully recognized famous faces in individuals with DP reflected the typical amplitude and scalp topography that is found for participants with unimpaired face processing abilities (see Gosling & Eimer, 2011), even though DPs recognized famous faces only on 27% of all trials. The presence of an N250 to non-recognized famous faces provides electrophysiological evidence for the existence of covert face recognition in developmental prosopagnosia. It is likely that the discrepancy between covert familiarity processing and overt recognition ability in the tested DPs arises from disrupted links between intact early perceptual and impaired high-level semantic face processing. In particular, while stored visual representations of familiar faces can be activated, as reflected by the presence of the N250 in a sub-set of the DP group, these representations appear to be disconnected from the final stages of face processing, resulting in an absent feeling of familiarity.

The finding of implicit familiarity processing in the absence of overt recognition by Eimer et al. (2012) demonstrates that face processing is a sequential multi-component process in which explicit face recognition depends on complete processing of each stage of the face processing hierarchy. Therefore, intact perceptual mechanisms are not sufficient to give rise to conscious familiarity if later semantic face processes are impaired. Instead, conscious recognition appears to require that faces are processed at post-perceptual stages, emphasizing a late locus of face-recognition impairments in some DPs (see Burton et al., 1991). In contrast, for those six DPs who showed no N250 component to non-recognized famous faces in the Eimer et al. (2012) study, the core face processing deficit appears to emerge during early perceptual face processing, reflecting either impaired structural face representations and/or poor representations of individual faces in visual memory. Moreover,

the degree of covert face recognition in prosopagnosia seems to be related to the degree of residual overt familiarity, suggesting that overt and covert face processes are related phenomena, which are mediated by the same underlying mechanism (Barton, Cherkasova, & O'Connor, 2001). This is further supported by Schweinberger and Burton (2003), who reported that individuals with more severe face recognition deficits are less likely to show covert recognition, indicating that covert face processes require a degree of spared functional normality. Electrophysiological evidence for residual normality of familiar face recognition in DP is in line with findings from neuroimaging studies. Avidan, Hasson, Malach, and Behrmann (2005) found normal patterns of fMRI activation in response to individual faces in the fusiform gyrus (including the FFA), as well as in ventral occipito-temporal regions in a group of four DPs, which were not differentiable from control participants. These findings suggest that neural activation in "core" face-selective regions is not sufficient for effective face recognition. Instead, it is the integrity of the whole face processing network, in particular of links between the core face-selective regions and the extended face network consisting of anterior temporal and frontal areas that appears crucial for successful face recognition (see Avidan & Behrmann, 2009).

Covert markers of unfamiliar face recognition

The research reviewed so far has addressed the neural basis of familiar face recognition. An interesting related question concerns the nature of unfamiliar face recognition processes in individuals with prosopagnosia. In AP, face recognition impairments are often manifested as an inability to learn new faces that have been encountered after the onset of the condition. While most covert face recognition studies have used familiar faces, there is some evidence suggesting that patients with AP can recognize at least some aspects of unfamiliar faces, including identity-related information, at an unconscious or implicit level. For example, De Haan, Young, and Newcombe (1991) demonstrated a patient with AP, who performed at above-chance level in selecting a previously seen face among two simultaneously presented unfamiliar faces, despite the absence of conscious identification of those faces. Similarly, Greve, and Bauer (1990) reported the spared ability of an acquired prosopagnosic to identity the 'previously seen' unfamiliar face among two images, of which one had been briefly presented during an implicit exposure phase prior to the recognition test. Overall, these

findings demonstrate the spared ability in some individuals with AP to perceive and encode identity-specific visual information from faces even when these are unfamiliar.

In research on unfamiliar face recognition, a distinction has been made between image learning as compared to identity learning (Burton & Jenkins, 2011). When identical images are repeatedly presented, face recognition can solely rely on matching low-level pictorial information about a face. In contrast, when different images of the same individual are shown, reliance on image-based visual cues is not sufficient but more abstract high-level information about the identity of a face needs to be extracted. While same-image matching is an effortless task in typical adults, unfamiliar face matching across different images is difficult even for individuals with intact face recognition abilities (e.g., Bruce et al., 1999). A related phenomenon has been observed for individuals with prosopagnosia. While simultaneous matching of two unfamiliar faces was essentially unimpaired in some APs, speeded sequential presentation resulted in markedly poor recognition performance (e.g., Benton & Van Allen, 1972; De Renzi, 1986). The finding of normal face matching abilities in APs when two faces are presented simultaneously has been attributed to the use of a slow feature-by-feature matching strategy that is available when unfamiliar faces are simultaneously present, thereby compensating for inefficient global structural face processing. In contrast, such a local part-based matching strategy is less useful for individuating two sequentially presented faces. Given the difficulty in matching sequentially presented faces, what might be the locus of this deficit? Matching two faces presented in rapid succession requires explicit access to a detailed representation of the identity of the first (no longer present) face in visual working memory (WM). The critical impairment in prosopagnosia might therefore concern this explicit access, that is, the successful match between an on-line face and its corresponding visual face memory trace. Furthermore, several lines of evidence suggest that face identity matching in prosopagnosia reflects an underlying impairment in the perception of global-holistic processing (see Section 1.6.1, for a more detailed review). Accordingly, perceiving and encoding the identity of unfamiliar faces may be particularly impaired across pictorial changes (such as changes in facial expression or view), which rely on holistic-configural face processes for the extraction of invariant face structure.

Bobes et al. (2003) demonstrated electrophysiological evidence for covert matching of the identity of unfamiliar faces in an acquired prosopagnosic. In this study, a patient with acquired prosopagnosia and a group of control participants performed an explicit face-

identity matching task, where two faces on each trial showed either the same or two different persons. The two images in a pair always differed in emotional expression to ensure that information about identity-invariant face structure above and beyond purely image-based information had to be extracted. Despite an inability of the individual with AP to explicitly match the identity of individual faces, reliable enhanced negativities were elicited at posterior electrodes on trials where two faces depicted two different as compared to the same person. The presence of reliable identity-specific ERP modulations in an acquired prosopagnosic, thought to reflect early matching based on face structure, can be explained if these early perceptual face processing stages are not affected. A later enhanced negativity was elicited at ~500 ms to repetitions of the same face in both the AP participant and the control group, and has been linked to covert matching based on visual semantic codes (Bobes et al., 2003). Overall, these findings are consistent with intact abstract processing of holistic-configural face structure in AP, while overt matching of sequentially presented faces may require explicit access to short-term memory of the first (no longer present) face. However, image changes in this study were restricted to subtle variations in local features (e.g., differences in facial expression), which may still have allowed the use of low-level pictorial cues as the basis for face matching. Therefore, a different pattern of results may emerge for sequential repetitions of two unfamiliar faces across changes in viewpoint, which markedly alter the global face structure.

Unlike APs, individuals with DP may never acquire typical representations of individual faces, which could imply that long-term face memories may be completely absent (Barton et al., 2001). However, the presence of covert neural responses to familiar faces in some DPs indicates that this condition does not always result from an inability to acquire individual face representations, but in some cases from a failure to gain access to visual-perceptual face memories. Therefore, the possibility remains that early visual stages of unfamiliar face processing (i.e., early perception and visual face memory) are intact in individuals with DP, even when two unfamiliar faces are shown in different views and view-independent face representations need to be formed (but see Towler et al., 2012, for electrophysiological evidence for atypical early perceptual face processes in DPs).

Research aims

The aim of Experiment 8 was to investigate the presence and nature of unfamiliar face recognition processes in individuals with DP in an *implicit* view-matching task. Two sequentially presented faces showed either the same or two different individuals, in either the same or two different views. In people with typical face recognition abilities, presenting two faces of the same person in rapid succession triggers an N250r component, which reflects the match between a seen face with a representation of the first presentation of that face in visual short-term memory. If early visual processing is impaired in some DPs, this should be reflected by an atypical or absent N250r component. Moreover, while typical adults show a reliable N250r across both view-repetitions and view-changes (see Chapters 2 and 3) DPs might show atypical neural responses on trials with a view-change, which requires the perception of view-invariant identity-specific codes from unfamiliar faces. As explicit face identity matching tasks are hard and frustrating for DPs, and may impair motivation over longer time periods, an *implicit* view-matching task was employed in the present study. This task required same/different view judgments on pairs of sequentially presented faces. Although no explicit face identity judgments are involved, the fact that this task requires relational judgments about the view of two sequentially presented faces is sufficient to elicit a clear N250r in participants with typical face recognition (see Experiment 3).

8.1.2 Method

Participants

DP group. Ten participants with DP (eight females), aged 29 to 56 years (mean age 46 years, SD = 10) were tested. All reported severe difficulties in face recognition since childhood, and were tested on a series of behavioural tests to assess and verify their reported face recognition problems. Table 8.1 shows z-scores of the performance of all 10 individuals with DP in two of these tests. In the Cambridge Face Perception Test (CFPT), six faces in a front view have to be sorted according to the degree of perceptual match with a target face shown in a side view. In the Cambridge Face Memory Test (CFMT), faces of six target individuals are learned, and then subsequently identified among two simultaneously presented distractor faces (see Duchaine & Nakayama, 2006). The CFMT is a standard test measuring both face perception and immediate visual face memory for unfamiliar faces. For each target face, three test items show identical views to those studied, five present novel

images (e.g., a change in view, lighting or both), and four present novel views with added noise.

Table 8.1 Details of the DP group

Participants	Age	Gender	CFMT-total	CFMT -1	CFMT-2	CFMT-3	CFPT
S.N.	54	F	-2.26	0.41	-2.49	-1.83	-2.15
Y.N.	43	F	-2.14	0.41	-2.72	-1.33	-2.29
C.T.	38	F	-2.64	-1.86	-2.72	-2.08	-1.19
C.M.	29	M	-4.29	-26.86	-3.88	-1.33	-3.10
A.C.	48	F	-2.77	-6.41	-2.72	-1.83	-4.06
M.Z.	49	F	-2.52	-1.86	-1.10	-1.83	-1.33
M.W.	56	M	-2.14	0.41	-2.96	-1.08	-1.60
R.G.	33	F	-3.02	-1.86	-3.65	-1.83	-2.29
S.M.	54	F	-1.25	-6.41	-1.10	-0.59	-2.01
H.P.	54	F	-2.26	-1.86	-2.03	-2.08	-1.74

List of the 10 individuals with DP who participated in the study, together with z-scores of each individuals' performance in the Cambridge Face Memory Test (CFMT), separately for each section (e.g., 1 = same images, 2 = novel images, 3 = novel images with noise), and the Cambridge Face Perception Test (CFPT). F = female; M = male.

All ten DPs showed impaired overall performance on the CFMT, in particular when target faces showed novel images (e.g., CFMT-2 and CFMT-3; see Table 8.1). In contrast, recognition of identical target images (CFMT-1) showed a large variability in scores, ranging from highly impaired to normal performance, which may reflect the successful reliance on low-level image matching strategies in some DPs. Similar patterns of impairments were observed on the CFPT. Nine participants were right-handed, and one was left-handed. All had normal or corrected-to-normal vision, and gave written informed consent prior to testing.

Control group. The control group consisted of ten adults (nine females), aged 23 to 54 years (mean age 34 years, SD = 10) with no subjective reports of face recognition deficits. All participants were right-handed and had normal or corrected-to-normal vision. Written informed consent was obtained before testing.

Stimuli and procedure

The stimulus set was identical to Experiment 3 (see Figure 8.1). Greyscale images of 30 unfamiliar faces (15 female faces) were shown in either a front view or a right-facing side view at an angle of approximately 45°. The visual angle subtended by the second face in each pair was always 20% larger than the second face to avoid identical stimulation of the same retinal areas on trials where the same face image was repeated. Images subtended an angular size of 6.9° x 4.3° (first face in a pair) and 8.0° x 5.2° (second face), and their average luminance was 7.7 cd/m^2. Faces were presented centrally against a light grey background (16.5 cd/m^2). There were 30 different identities, two different views and two different sizes, resulting in a total of 120 images. All stimuli were presented centrally on a CRT monitor at a viewing distance of 100 cm. E-Prime software (Psychology Software Tools, Pittsburgh, PA) was used for stimulus presentation and data collection.

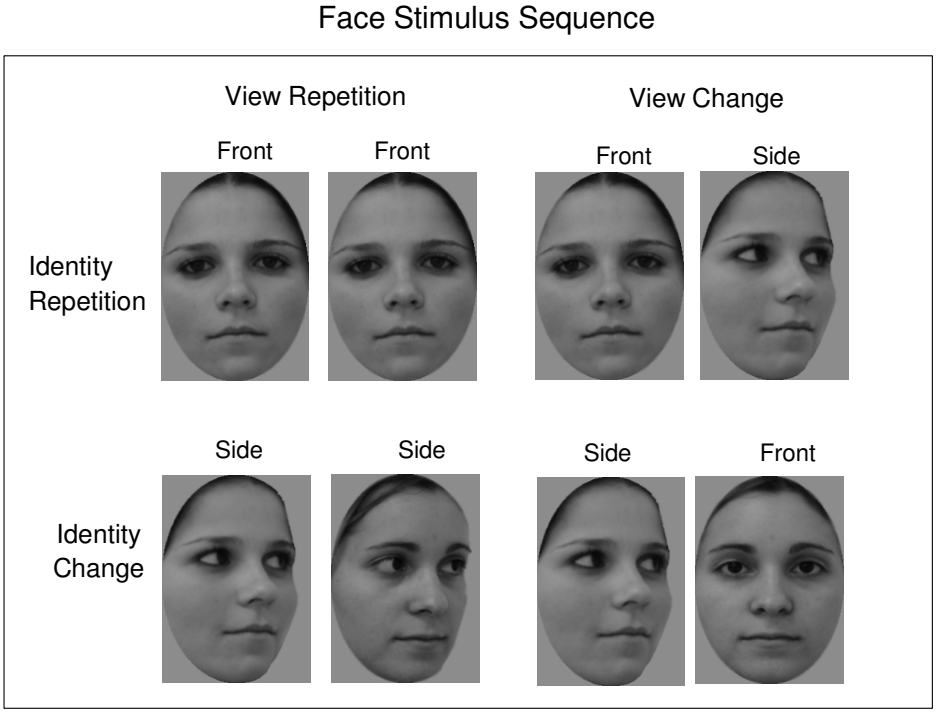


Figure 8.1 Examples of naturalistic face stimuli and the four different face stimulus sequences. Two faces showed either the same or two different persons (identity-repetition versus identity-change), in either the same view (front-front or side-side trials; view repetition) or a different view (front-side or side-front; view change). The second image was always 20% larger than the first image. Temporal parameters of stimulus presentation were identical to Experiments 1-5.

Temporal parameters of stimulus presentation were identical to those used in previous experiments. Each stimulus in a pair was present for 200 ms, separated by a 200 ms ISI. The intertrial interval was 1500 ms. Each face pair was equally likely to show the same or two different individuals, and the same or two different views. These two factors were varied orthogonally, with 20 trials per block for each combination of identity (identity-repetition versus identity-change) and view (view-repetition versus view-change). Participants performed same/different view judgments on sequentially presented face pairs. They were instructed to respond with a left-hand button press on trials where two faces showed the same view (regardless of identity), and with a right-hand button press when view changed between images. The experiment lasted about 25 minutes, and was preceded by one training block.

EEG recording and data analysis

EEG recording and data analysis were identical to previous experiments, except that EEG was recorded from 25 scalp sites including additional posterior electrode pair P9 and P10. Following artifact rejection, EEG waveforms were averaged separately for each combination of the factors identity (identity-repetition versus identity-change) and view (view-repetition versus view-change). Mean amplitude values were computed at posterior electrodes P9/10 for the N170 time interval (160-190 ms after the onset of the second face) and for the N250r time interval (220-280 ms after the onset of the second face). Repeated-measures analyses of variance (ANOVAs) were performed for the within-subjects factors identity and view, and the between-subjects factors group (DP versus control group). To assess the effect of face learning in the DP group only, N250r components were analyzed separately for the first half (blocks 1-4) and the second half (blocks 5-8) of the experiment. These analyses included the additional factor half (first half versus second half). It has to be noted that two DPs only completed 6 out of 8 experimental blocks due to tiredness. For those two DPs, ERP averages in blocks 1-4 (first half) were compared with those obtained for blocks 5-6 (second half). Learning effects could not be measured in the control group as these participants were already familiar with the stimulus set.

8.1.3 Results

Behavior

DP versus control group. Mean accuracy for the view-matching task was 93%, and there was no main effect of group ($F < 1$). Accuracy was higher for same as compared to different view judgments (94% versus 91%; $F(1,18) = 5.6$; $p < .04$), and on trials where two faces showed the same relative to two different identities (94% versus 91%; $F(1,18) = 11.8$; $p < .04$). An interaction between view and group approached significance ($F(1,18) = 3.8$; $p < .08$). Separate follow-up analyses were conducted for each group. In the DP group, a main effect of view approached significance (95% versus 91% for view-repetition versus view-change trials; $F(1,9) = 4.9$; $p < .06$), and this effect was absent in the control group (92% each; $F < 1$). There were no interactions between identity and group ($F < 1$), or between identity and view ($F(1,18) = 11.$; $p = .312$). There was also no three-way interaction (identity x view x group: $F(1,18) = 1.1$; $p =. 317$). Separate analyses were also performed on factor half (first versus second half of the experiment) for the DP group only. Results showed no main effect of half, and no interaction between identity and half (both $F < 1$), or a three-way interaction (identity x view x half: $F(1,9) = 1.4$; $p = .275$).

Mean correct RT was 585 ms, and there was no main effect of group ($F(1,18) = 1.3$; $p = .272$). Responses were faster on trials where both identity and view were repeated (535 ms) than on trials with a change of identity, a change of both attributes, or a change of view (595 ms, 604 ms, and 611 ms, respectively). This was reflected by main effects of view (565 ms versus 608 ms; $F(1,18) = 23.2$; $p < .001$), identity (573 ms versus 600 ms; $F(1,18) = 44$; $p < .001$), and a significant interaction between both factors (identity x view: $F(1,18) = 66.6$; $p < .001$). A view x group interaction approached significance ($F(1,18) = 3.3$; $p < .09$). This was followed up by separate analyses for each group: RTs were significantly faster on view-repetition as compared to view-change trials in the DP group (581 ms versus 639ms; $F(1,9) = 23.2$; $p < .01$), but this effect only approached significance in control participants (550 ms versus 576 ms; $F(1,9) = 4.3$; $p < .07$). The three-way interaction was not significant (identity x view x group: $F < 1$). Additional analyses performed for the factor half for the DP group only showed that overall RTs on the view-matching task were significantly faster in the second half of the experiment as compared to the first half (572 ms versus 646 ms; $F(1,9) = 5.4$; $p < .05$). There was no interaction between identity and half or between identity, view and half (both $F < 1$).

ERP markers of visual face memory: DP versus control group

Figure 8.2 (top panel) shows grand averaged ERP waveforms elicited at lateral occipital electrode pair P9/10 to identity-repetitions and identity-changes in the 400 ms interval after the onset of the second face. ERPs are averaged across all eight experimental blocks and across view-change and view-repetition trials, and are shown separately for the DP and the control group. Repetitions of the same face triggered characteristic bilateral N250r negativities over posterior electrodes, which were accompanied by a frontal positivity in the same latency range in both the DP and the control group (see Figure 8.2, bottom panel). A reliable N250r was not only elicited in control participants, but also in individuals with DP. However, even though a reliable N250r was elicited in both groups, this component was larger in control as compared to DP participants.

To test whether these group differences would by particularly pronounced on trials with a view change, ERPs were averaged separately for view-repetition and view-change trials, and for DP and control groups. On trials where the same view was repeated, a reliable N250r was present for both DP and control participants (see Figure 8.3, top panels). In contrast, on view-change trials, clear bilateral N250r components were elicited in the control group, but this component was strongly attenuated in the DP group (see Figure 8.3, bottom panels).

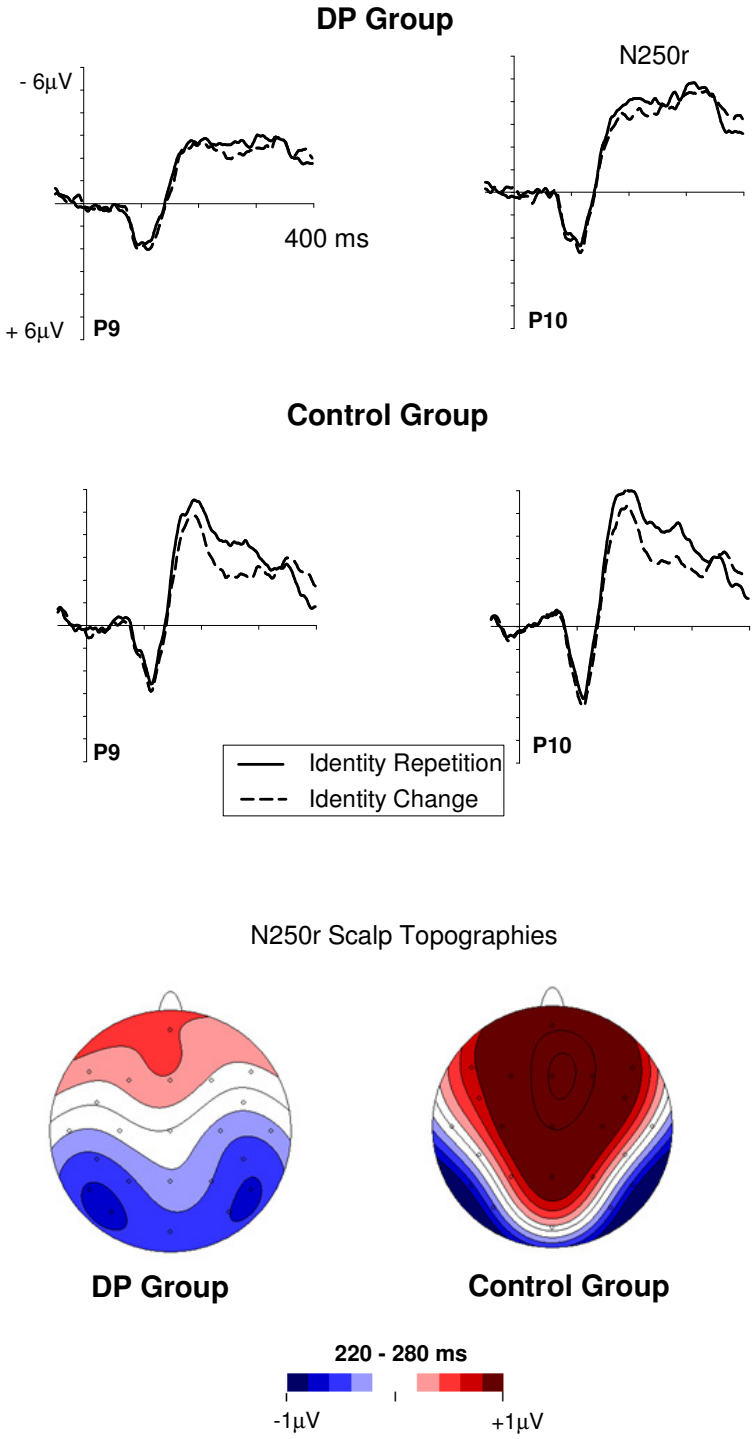


Figure 8.2 Top panel: Grand-averaged ERPs measured at lateral posterior electrodes P9/10 in the 400 ms interval after the onset of the second stimulus in a face pair for identity-repetition trials (solid lines) and identity-change trials (dashed lines). ERPs are shown separately for the DP and the control group, and are collapsed across view-repetition and view-change trials. Bottom panel: Topographic maps of N250r difference waves (identity repetition - identity change), separately for the DP and the control group.

Statistical analyses were conduced for lateral posterior electrode pair P9/10 where the N250r was largest. Clear N250r components were obtained in the 220-280 ms time window after the onset of the second image in each face pair ($F(1,18) = 14.4$; $p < .01$). Even though the N250r was numerically larger in the control group as compared to the DP group (see Figure 8.2, top panel), an identity x group interaction did not reach significance $F(1,18) = 3$; $p = .101$). An interaction between identity and view ($F(1,18) = 4.5$; $p < .05$) suggested that N250r amplitudes were modulated by view, but a three-way interaction was not significant (identity x view x group: $F < 1$). Separate analyses were performed for view repetitions as compared to view changes. On view-repetition trials, a clear N250r was elicited ($F(1,18) = 13.4$; $p < .01$), but there was no interaction between identity and group ($F(1,18) = 1.2$; $p = .283$). A different picture emerged for view-change trials: Here, a main effect of identity ($F(1,18) = 2.7$; $p < .02$) was accompanied by a nearly significant interaction between identity and group ($F(1,18) = 4.4$; $p < .06$).

To directly compare N250r components elicited on view-repetition and view-change trials, separate analyses were performed for DP and control participants. For the control group, there was a main effect of identity ($F(1,9) = 8.7$; $p < .02$), but no identity x view interaction ($F(1,9) = 2.3$; $p = .161$). Follow-up analyses were conducted for each level of the factor view, and these showed a clear N250r on both view-repetition trials ($F(1,9) = 9.0$; $p < .02$) and view-change trials ($F(1,9) = 6.0$; $p < .04$) for control participants, confirming previous findings that the N250r is view-invariant in adults with typical face recognition. For the DP group, a clear N250r component was elicited by repetitions versus changes of identity ($F(1,9) = 8.3$; $p < .02$). An interaction between identity and view was not reliable in DP participants ($F(1,9) = 2.3$; $p = .167$), and separate analyses for each level of the factor view showed that the N250r approached significance on view-repetition trials ($F(1,9) = 4.5$; $p < .07$), but was absent on view-change trials ($F(1,9) = 1.5$; $p = .246$).

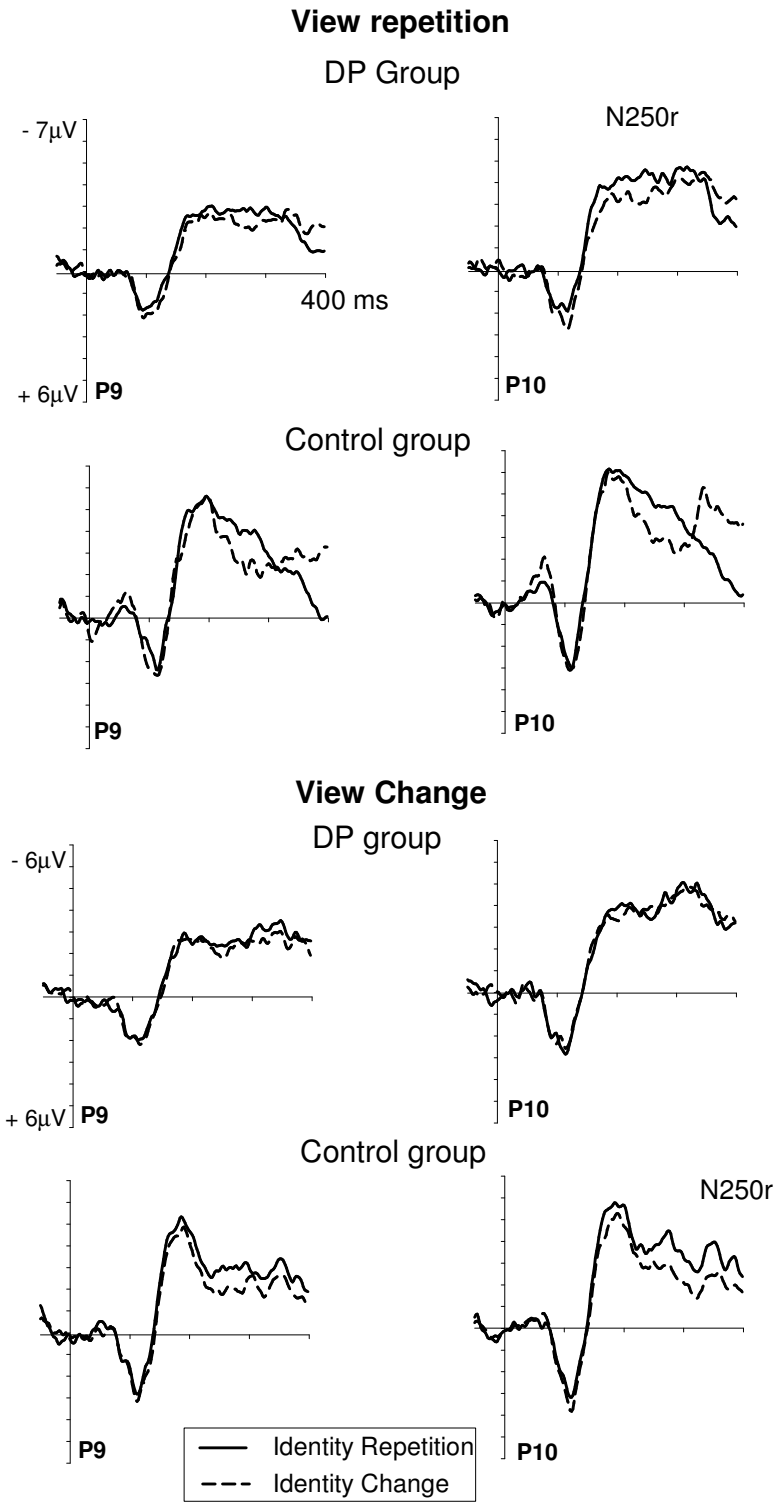


Figure 8.3 Grand-averaged ERPs at posterior electrode pair P9/10 in the 400 ms interval after the onset of the second stimulus in a face pair for identity-repetition trials (solid lines) and identity-change trials (dashed lines). ERPs are shown separately for view-repetition (top panels) and view-change trials (bottom panels), and for the DP and the control group.

Face learning in DPs: First versus second half

To assess the impact of learning on face recognition processes in DP participants, ERPs measured in the first half of the experiment (blocks 1-4) and the second half (blocks 5-8; blocks 5-6 for two individuals with DP) were analyzed separately. As shown in Figure 8.4, clear N250r components emerged in the second half of the experiment collapsed across factor view. In contrast, an N250r in the first half of the experiment is visible, but is strongly attenuated as compared to the second half. An increase in the occipital negativity over posterior electrodes (N250r) in the second as compared to the first half of the experiment is further demonstrated in Figure 8.4 (bottom panel), showing scalp topographies of N250r difference amplitudes calculated by subtracting ERPs on identity-change trials from ERPs on identity-repetition trials.

A clear N250r was present at posterior electrode pair P9/10 ($F(1,9) = 9.9$; $p = .012$), but there was no interaction between identity and half ($F(1,9) = 1.6$; $p = .242$), or a three-way interaction (identity x view x half: $F < 1$). Separate analyses were conducted for ERPs measured during the first half and the second half of the experiment. The N250r in the DP group was too small to reach significance in blocks 1-4 ($F < 1$), and only reliably emerged in the second half of the experiment (blocks 5-8; $F(1,9) = 21.7$; $p < .01$). An absent identity x view interaction in the second experiment half ($F(1,9) = 2.5$; $p = .146$) indicated that the N250r was view-invariant, and follow-up analyses confirmed the presence of an N250r on both view-repetition ($F(1,9) = 12.3$; $p < .01$), and on view-change trials ($F(1,9) = 6.1$; $p < .04$).

This was further assessed in separate analyses for view-repetition and view-change trials. For view-repetition trials, a main effect of identity approached significance ($F(1,9) = 4.8$; $p < .06$), but there was no interaction between identity and half ($F < 1$). A different picture emerged on view-change trials: Here, there was no main effect of identity ($F(1,9) = 2.2$; $p = .174$), but a significant interaction between identity and half ($F(1,9) = 6.8$; $p < .03$), indicating that on those types of trials, an N250r only reliably emerged during the second half of the experiment, but was absent during the first experimental half.

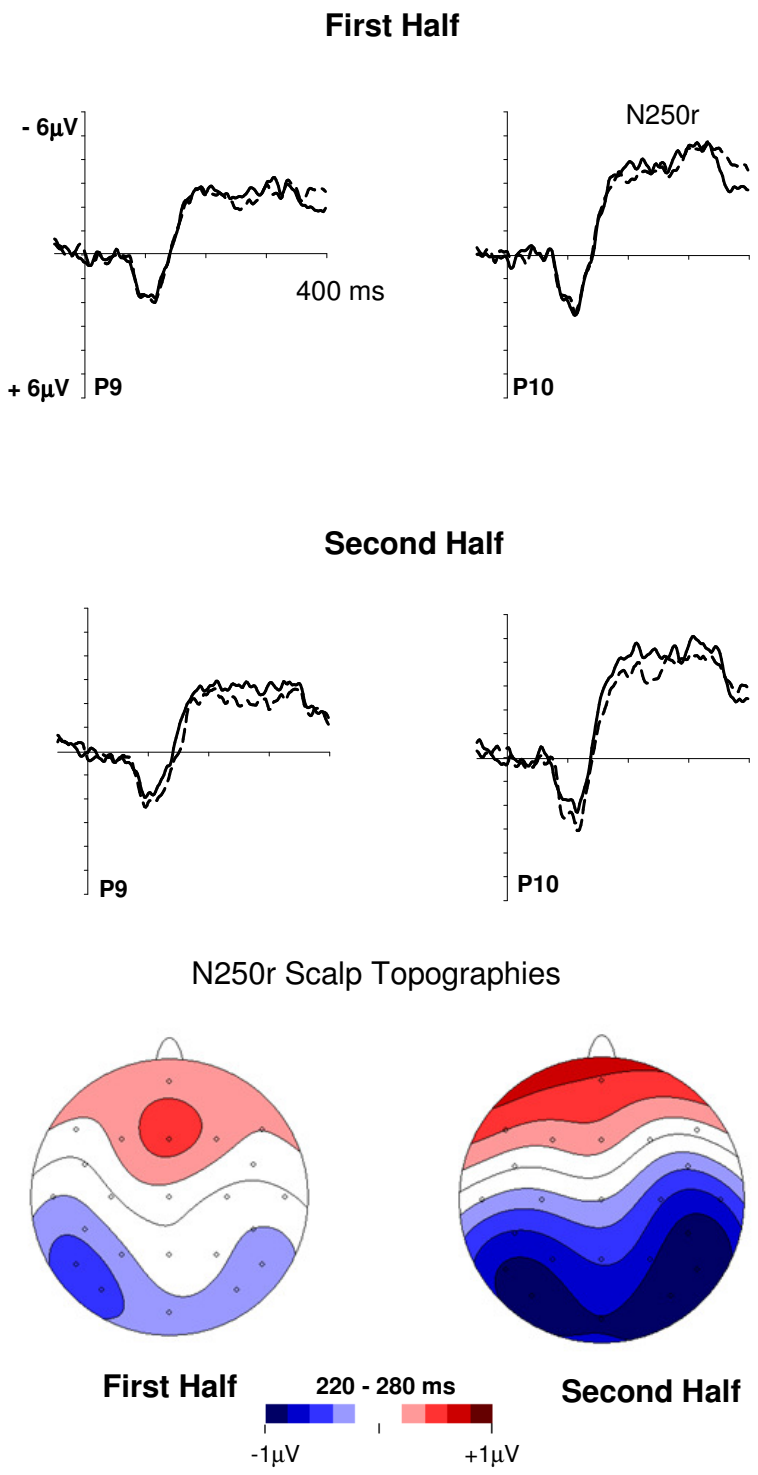


Figure 8.4 Top panel: Grand-averaged ERPs for the DP group, collapsed across view-repetition and view-change trials. ERPs are shown separately for the first half (blocks 1-4) and the second half (blocks 5-8 in eight DPs; blocks 5-6 in two DPs). Bottom panel: Topographic maps of N250r difference waves (obtained by subtracting identity-change from identity-repetition trials), separately for first and second half. Enhanced negativities are shown in blue, enhanced positivities in red.

8.1.4 Discussion

The aim of Experiment 7 was to test the presence and nature of unfamiliar face recognition processes in a group of ten DPs in an *implicit* task that required same/different view judgments of sequentially presented face pairs. On each trial, two images were presented in rapid succession, and these either showed the same or two different individuals, in either the same or two different views. Two research hypotheses were tested: First, if early visual face processes are intact in some DPs, this should be reflected by the presence of an N250r component to same face repetitions. On the contrary, the finding of an atypical or even absent N250r in DP participants would indicate an underlying difficulty to extract identity-related visual information from unfamiliar faces in a task where identity is irrelevant. Second, if an N250r is present in DP participants on view-repetition trials (where two images share low-level perceptual features) but not on view-change trials, this would indicate an underlying perceptual impairment in extracting more abstract visual cues about individual identity. In addition, ERP waveforms in DP participants were computed separately for the first half (blocks 1-4) and second half (blocks 5-8) of the experiment to investigate implicit face learning in DP.

Analyses of ERP data collapsed across all experimental blocks demonstrated that a reliable N250r component was elicited in control participants by repetitions of the same individual face (irrespective of the view in which it was shown), which emerged between 220-280 ms after the onset of the second face in a pair. The presence of an N250r in typical adults during an implicit view-matching task is consistent with previous findings from Experiment 3 of the present thesis. Importantly, an occipito-temporal N250r was also reliably triggered in the DP group. This is exactly the finding that would be expected if early face perception and visual working memory are spared in some individuals with DP (see Figure 8.2, top panel), suggesting a spared degree of functional normality during early face processing stages despite severe face recognition deficits in the same individuals in daily life. Moreover, scalp topography and onset latency of the N250r component were very similar for both individuals with intact face recognition abilities and developmental prosopagnosics (see Figure 8.2, bottom panel). These findings provide electrophysiological evidence for the implicit processing of unfamiliar face identity in a view-matching task in a group of ten DPs, demonstrating intact neural processes for the perception of individual identity even when face stimuli are unfamiliar and shown from different views. This indicates that a degree of

spared functional normality in DP does not only apply to implicit recognition of famous faces (see Eimer et al., 2012, for implicit processing of famous face identity) but also applies to the learning of new unfamiliar face identities. Thus, the present data go beyond findings from Eimer et al. by showing that identity-related facial cues are already extracted following very few encounters with initially novel unfamiliar faces. This challenges the hypothesis that a general deficit in the visual aspects of identity-related processing underlies all types of prosopagnosia (Farah et al., 1993). Instead, the current findings are compatible with a neuropsychological account of developmental prosopagnosia, which proposes a degree of spared perceptual face processing mechanisms and localized impairments to distinct sub-components or connecting links. Applied to the tested ten DPs in the present experiment, severe face recognition deficits may arise due to disrupted links between intact perceptual face memories and semantic memories that enable conscious familiarity. This explanation is consistent with the 'disconnection hypothesis', which assumes that weakened connections between intact processing stages give rise to severe face recognition impairments (Burton et al., 1991; see also De Haan et al., 1991).

The aim of Experiment 7 was to test whether reliable N250r components would be elicited in DPs, and whether these would not only be present on trials where the same face was repeated in the same view, but also on trials with a view change. On the latter type of trials, identity processing is assumed to be based on the acquisition of an invariant identity-specific face representation compared to mere reliance on image-based pictorial information. Accordingly, DPs should be unable to rely on a local feature-matching strategy but need to use global-holistic face processing in order to extract identity-sensitive information from a face. Visual inspection of N250r amplitudes for identity-repetitions versus changes, separately for DP and control participants, showed that this component was clearly elicited in both groups. However, analyses for DP and control group, separately for view-repetition and view-change trials suggested a differential effect of factor view on N250r amplitudes. On view-repetition trials, an N250r of similar size was triggered for both DP and control groups. In contrast, a different picture emerged for view-change trials: Here, a reliable N250r was elicited for control participants, but this component appeared to be strongly attenuated in the DP group (see Figure 8.3, bottom panels), suggesting differences between the two groups in the ability and/or efficiency to extract invariant aspects of facial identity. Thus, whereas adults with unimpaired face recognition abilities can effortlessly extract identity-related

information across image transformation such as view changes, the ability to extract invariant face structure seems to be impaired in some DPs. If this is correct, a selective perceptual deficit to encode holistic-configural information may underlie face recognition deficits in some DPs, resulting in the failure to acquire a sufficiently detailed perceptual memory trace of the first face that allows subsequent recognition of the same person shown in a different view. However, this conclusion needs to be qualified, as the relevant interaction between identity and view for the N250r component in the DP group was not significant, presumably due to large interindividual differences between DPs in the effect of view changes on the N250r.

Unfamiliar faces were used in the present study with which DP participants became familiar in the course of the eight experimental blocks. An interesting question concerns whether N250r responses in DPs are modulated by repeated exposure to initially novel unfamiliar faces, indicative of implicit identity learning. If repeated exposure to the same facial identities in the course of the experiment results in qualitative changes in the underlying neural response, this should be reflected by the emergence of a clear N250r only in the second experimental half when novel face have become more familiar. As the experimental task did not require explicit identity matching, it is difficult to predict whether or not the implicit nature of the task might have resulted in a general slowing down of face learning processes. Previous findings from Experiment 2 of the present thesis (see Chapter 4) demonstrated perceptual mechanisms of face learning in typical adults during an explicit identity-matching task, where a qualitative change in the ERP response to same face repetitions emerged as a result of increasing familiarity. In this experiment, an N250r was absent during the first half of the experiment on trials with a view change, but reliably emerged during the second experimental half. In contrast, N250r components were present for both first and second experimental half on view-repetition trials. It is unclear whether a similar pattern of perceptual learning would be observed in typical adults in a task context where view and not identity is the to-be-attended facial feature.

An analysis of ERP data for the DP group only, separately for the first and second experimental half, demonstrated a modulation of the N250r response as a result of face learning. The N250r tended to be more reliable in the second half of the experiment as compared to the first experimental half, irrespective of the view in which two faces were shown. The emergence of a more reliable N250r in the second half of the experiment after

repeated exposure to novel faces provides electrophysiological evidence for intact perceptual face learning in individuals with DP. These results demonstrate a modulation of N250r amplitudes same face repetitions during learning, which was not only found for trials where two faces showed the same view, but also on trials with a view change. This suggests that even though DPs appeared to have difficulties to extract identity-specific information on trials with a view change, ERP evidence indicated intact learning of abstract identity-specific information. However, it must be acknowledged that the interaction between identity and half was not significant for the DP group. Therefore, the exact nature of neural mechanisms of face learning in DP needs to be further clarified in future studies. As control participants were already familiar with the face set, a direct comparison of learning-related N250r responses between DP and control participants was beyond the scope of the present study and needs to be addressed in future research.

In contrast to most previous N250r studies, which involve explicit identity judgments, the present study employed a view-matching task while measuring implicit neural markers of unfamiliar face recognition. In this context, the presence of reliable N250r markers of unfamiliar face recognition and face learning in ten individuals with DP is even more remarkable, given that the task required judgments about the specific view in which a face was shown and not about its identity. Even though explicit processing of unfamiliar face identity was not required to perform the task, the presence of an N250r demonstrated that participants had encoded a detailed visual face memory trace to the first face that not only contained information about the overall shape (e.g., the specific view in which the face was shown), but also detailed information about identity-sensitive face structure (see Experiment 3, for similar findings). Importantly, this was the case in both adults with typical face recognition abilities and participants with DP. This finding suggests that sequential judgments about two face images in memory is sufficient to generate a visual-perceptual face memory of that individual, and that identity-related visual aspects of unfamiliar faces are under those conditions processed in an obligatory way and regardless of current task demands. Thus, learning unfamiliar face identities occurs to some degree automatically, even in DPs.

What insights do the current findings provide about the neural architecture that underlies unfamiliar face perception and recognition in developmental prosopagnosia? The present study provides electrophysiological evidence for both spared face perception and visual short-term memory, which are essential to individuate faces during rapid sequential presentations.

These findings not only suggest a degree of spared functional normality of unfamiliar face recognition, but also a degree of automaticity of identity-related processing during implicit matching tasks. In addition, the observation that DPs show a typical but numerically smaller N250r component to same face repetitions across view changes suggests that their recognition deficit is not linked to an inability to acquire high-level abstract representations of individual faces, but is likely to reflect an inefficiency to process invariant structural aspects of faces. Such an interpretation would also explain the low scores in the DP group on the CFMT, which requires the recognition of newly learned faces among novel images. Furthermore, the similarity of the observed unfamiliar face recognition processes in both individuals with DP and controls indicates that there are no fundamental qualitative differences in the underlying face recognition architecture during early perceptual stages of face recognition.

How can these data be interpreted in terms of Bruce and Young's (1986) face recognition architecture? The present data suggest that face recognition deficits do not always arise from defective early face-selective visual processes but may indicate deficient access to stored memory representations of individual faces. Such an interpretation implies that some face-selective neural processes are spared in prosopagnosia, closely mirroring those of typical adults (see Burton et al., 1991; Eimer et al., 2012). The presence of such sparing of early perceptual face mechanisms in DPs could therefore be linked to a partly normally functioning 'structural encoding' stage, reflecting the successful extraction of high-level abstract information for facial identity (e.g., structural codes). In the context of Bruce and Young's model, in some DPs intact visual-perceptual face representations, or FRUs, are formed, but face recognition deficits are likely to arise largely due to a failure during later post-perceptual face processing stages. More specifically, once early visual codes have been extracted, those need to be converted into semantic person identity nodes, or PINs, that, when activated, result in explicit face recognition and a conscious feeling of familiarity. Even though information about unfamiliar faces contained in PINs can only be restricted to very few observable semantic details (e.g., gender or age), or associations (e.g., attributes about a person inferred from his or her face), activation of those semantic codes appears to be crucial for successful recognition. In line with Burton's (1991) model, links between permanently (in the case of familiar faces) or temporary (in the case of unfamiliar faces) visual face memories (FRUs) and acquisition of or access to semantic face memories (PINs) are impaired in individuals with DP. This functional interpretation of DP is consistent with the 'associative

type' of prosopagnosia (De Renzi et al., 1991), where deficits are unrelated to face perception and visual short-term memory, but arise at more high-level abstract processing stages where visual memory is linked to semantic memory and conscious familiarity.

The assumption of DP as a disconnection phenomenon is compatible with the view of a disconnection between posterior regions of the "core" face recognition system and more anterior temporal and frontal regions, which form part of the "extended" face processing system (Haxby et al., 2000). If this is correct, it would suggest that there is no generalized damage to early structural face processing in developmental prosopagnosia, but that severe face recognition deficits can arise from a failure of temporarily (or permanently) stored visual representations of faces to be converted into semantic face memories and/or conscious access to those memory traces. This would also explain the dissociation between impaired overt face recognition ability and spared perception and visual short-term memory for faces in DP, with each reflecting different stages of face processing (see Eimer et al., 2012). While overall recognition performance is based on a completed sequence of successful face processing stages (e.g., perceptual and post-perceptual), neural markers highlight a degree of spared normality during early perceptual face processing stages only.

In summary, the current experiment provides, for the first time, electrophysiological evidence for spared perceptual stages of unfamiliar face recognition and face identity learning in ten individuals with developmental prosopagnosia in an implicit view-matching task. N250r components to same face repetitions in DP participants closely mirrored those of a control group, indicating underlying intact neural mechanisms of face perception and visual short-term memory in DPs. Importantly, an N250r was not only elicited in the DP group on trials where the same view was repeated, but also on trials with a view change. However, N250r amplitudes on view-change trials tended to be attenuated in DPs, suggesting inefficient functioning neural mechanisms for the perception of identity-specific invariant aspects of faces. In addition, the N250r was more reliable in the DP group during the second half of the experiment when initially unfamiliar faces had become more familiar, indicative of perceptual face learning. Taken together, the results support the view that face recognition deficits in DP can be described in terms of localized impairments that can selectively affect late post-perceptual stages of semantic processes while early visual stages of face recognition function, to some extent, in a typical fashion. These findings highlight the role of post-perceptual face

processing stages, where semantic person-specific face memories are activated, for explicit face recognition.

Chapter 9. Conclusions

9.1 A brief synopsis

Faces are "special" not only because we possess expert visual skills to recognize them, but most importantly in terms of their social relevance for human interactions. However, little consensus had been reached about whether or not faces are processed by specialized neural mechanisms or 'modules' (Farah, 1996; Kanwisher et al., 1997). An alternative explanation is that our expertise in recognizing faces is attributable to life-long exposure to faces, resulting in the recruitment of dedicated perceptual processes for stimuli of expertise (Diamond & Carey, 1986). In the past decades, cognitive psychology, neuroscience and clinical neuropsychology have each provided important insights into the cognitive mechanisms of face recognition, and their underlying neural basis. These suggest that a complex neural network mediates human face perception where different aspects of faces are processed in separate processing streams within a sequential and hierarchical system. The classic Bruce and Young (1986) model distinguishes between different types of codes that can be extracted from faces including two types of visually derived codes. *Pictorial* codes reflect changeable low-level image-based information while *structural* codes contain invariant facial features that are essential for successful face recognition.

The notion of a distributed neural system for face recognition has received further support from neuro-anatomical models (e.g., Haxby et al., 2000; Ishai et al., 2005). These distinguish between "core" and "extended" systems for face perception. The core visual regions of the face network are made up of three occipito-temporal areas that mediate the visual analysis of faces: the occipital face area (OFA), the fusiform face area (FFA), and the posterior superior temporal sulcus (pSTS). While the OFA is thought to represent the entry point for the early perception of facial features, FFA and pSTS represent parallel processing pathways for the processing of invariant identity-specific or dynamic social cues, respectively. The extended system consists of additional regions that are involved in the processing of non-visual information from faces. Thus, face recognition is thought to proceed along a serial processing stream, from low-level visual analysis up to high-level processing for detailed perceptual and semantic analysis. The current thesis is an investigation of the brain mechanisms underlying the perception and recognition of unfamiliar faces (i.e., faces that we have only seen a few times). In particular, several open questions about the view-dependence or independence of

unfamiliar face recognition processes were explored, as well as the role of strategic processing (i.e., attention) and WM maintenance on face identity processing.

In recent years, most face perception research has focused on investigating the neural mechanisms mediating familiar face recognition, while little is known about the neural processes that underlie our ability to recognize unfamiliar faces. Evidence from cognitive psychology and neuropsychology suggests that visual face recognition processes for familiar and unfamiliar faces rely on qualitatively different neural mechanisms that mediate both the visual analysis and memory representation of individual faces (e.g., Burton & Jenkins, 2011). Face memory studies have shown that unfamiliar face recognition is poor when different images of the same person are used between learning and test, while familiar face recognition is largely invariant to such low-level *pictorial* changes (e.g., Bruce et al., 1999; Burton et al., 1999). Moreover, some brain-damaged patients show a spared ability to identify familiar faces but are unable to learn new faces, and the reversed pattern of intact learning of unfamiliar faces despite severe problems in recognizing known faces has also been reported (Malone et al., 1982). In contrast to such clear behavioural discrepancies between recognition memory for familiar and unfamiliar faces, there is little systematic research into its neural basis. Most fMRI research did not find reliable qualitative differences in FFA activity to familiar relative to unfamiliar faces, suggesting that differences in recognition ability may be quantitative rather than qualitative (see Natu & O'Toole, 2011, for a review).

In contrast to fMRI research, ERP measures are able to reflect transient changes in neural responses to faces as a function of pre-existing or experimentally acquired familiarity within a time range of a few hundred milliseconds. ERP research has shown that repetitions of the same individual reliably elicit N250r negativities over occipito-temporal regions, which are typically larger for familiar than for unfamiliar faces (e.g., Schweinberger et al., 1995; 2002). These are thought to index the re-activation of identity-specific facial information in visual memory when the same individual face is repeatedly presented (Schweinberger & Burton, 2003). Similarly, N250 components are triggered to the first presentation of a familiar face (Gosling & Eimer, 2011), and these also emerge to initially unfamiliar faces as a result of face learning (Tanaka et al., 2006). Thus, N250/N250r components are thought to represent neural markers of face familiarity reflecting the strength of the visual memory representation of an individual face. Moreover, the presence of N250/ N250r responses across various image transformations suggests that the underlying face representations are not purely based on

pictorial information but on more abstract visual information about the structural components of a face that are essential for recognition (e.g., Schweinberger et al., 2002; Bindemann et al., 2008).

To better understand face recognition, it is necessary to identify not only which brain structures are involved but also the temporal dynamics of the neural activity in these regions. The series of experiments reported in the present thesis combined behavioural and ERP measures to investigate the brain mechanisms that underlie our ability to perceive and recognize individual unfamiliar faces. All studies except for Experiment 6 employed rapid repetition paradigms where pairs of unfamiliar faces were presented in rapid succession for 200 ms each, separated by a 200 ms interstimulus interval (ISI). Unlike previous N250r research, this rapid paradigm was chosen to track the fast encoding and activation of newly acquired perceptual face memories. Repetitions paradigms were employed, as these represent a useful tool for studying stimulus selectivity of neural responses that reflect early visual face recognition processes that occur within 300 ms of stimulus onset. Statistical analyses focused on the occipito-temporal N250r ERP response as a neural marker of visual face memory elicited over posterior electrodes in the 200-300 ms time window. The N250r component was followed by an enhanced positivity to identity repetitions versus changes in the subsequent 300-400 ms time window assumed to reflect a decision-making process where repetitions of the same face indicate 'target' responses (e.g., a P3 component). This interpretation is in line with larger positivities on same-view as compared to different-view trials where identity judgments were significantly faster.

View-independent recognition and face learning

Humans effortlessly recognize familiar faces despite changes in their visual appearance. In contrast, identifying unfamiliar faces across different views or other image changes (e.g., facial expression or ageing) poses a challenge for our face processing system. How doe we recognize the same individual face across very different visual inputs? Bruce and Young (1986) propose that successful face recognition is based on the extraction of high-level abstract visual information about the structural aspects of a face. These *structural codes* represent the essential properties of a face that distinguish it from other faces, and are invariant across low-level image-related changes. However, the exact nature of these identity-specific codes and their acquisition during face learning is still largely unknown. One

hypothesis is that repeated exposure to the same novel unfamiliar face results in qualitative changes in the way in which strictly unfamiliar and 'visually learned' faces are processed and represented in human visual cortex. This is in line with the assumption that unfamiliar face recognition is largely based on low-level *pictorial* codes, whereas the identification of familiar faces relies on stable identity-specific *structural* codes (Hancock et al., 2000). This is supported by behavioural evidence from face matching studies where poor recognition memory is observed for unfamiliar but not familiar faces when the same face is show from different photographs, suggesting that unfamiliar face recognition processes are largely based on image-specific visual cues (e.g., Burton et al., 1999). However, the finding of a reliance on pictorial cues after face learning from different photographs (Longmore et al., 2008) appears to challenge the view that more abstract identity-specific information is derived from faces during learning.

While behavioural evidence suggests that representations of unfamiliar faces are represented as snapshot-like images of the specific encounter, ERP research has demonstrated a degree of low-level invariance in unfamiliar face recognition. Repetition-related N250/N250r components are reliably triggered to repeatedly presented unfamiliar faces across different photographs (Kaufmann et al., 2008), as well as across changes in viewpoint (Caharel et al., 2009). Thus, ERP evidence suggests that perceptual representations of individual faces are to some extent based on high-level identity-specific information, and these representations gradually emerge to initially novel faces during learning (Tanaka et al., 2006). The assumption that some kind of abstract structural description of faces is formed also receives strong support from neuroanatomical models where the perception of invariant identity has been linked to neural activity in the lateral fusiform gryrus (Haxby et al., 2000; Grill-Spector et al., 2004).

The first two experiments of the present thesis outlined in Chapters 3 and 4 investigated the nature of visual memories that are acquired during rapid face repetitions of the same unfamiliar face, shown from different viewpoints. While previous research has shown that newly acquired face representations are not purely based on low-level pictorial codes, it is not clear whether the underlying perceptual mechanisms also generalize across large changes in view (e.g., a change from a front view to a profile view). Experiment 1 (see Chapter 3) tested whether neural markers of explicit face recognition would emerge to rapidly presented pairs of unfamiliar faces during explicit face identity matching. To investigate the view-

dependence or independence of face recognition processes, face stimuli were shown in three different views: front, side (rotated by 45°), or profile. On half of all trials, two faces showed the same individual, and on the other half two different individuals were presented. Face view always changed between repetitions, and trials consisted of either small or large rotations in viewing angle (45° versus 90°) to assess whether N250r amplitudes would be modulated by the relative angle of rotation. A reliable N250r was triggered by rapid repetitions of unfamiliar faces despite the view change on each trial, demonstrating the view-invariance of the underlying face representations. Moreover, N250r amplitudes were unaffected by the relative degree of rotation. This not only confirms previous findings of view-independent face recognition but also demonstrates fast extraction of and access to identity-specific codes, even when faces are unfamiliar.

One limitation of Experiment 1 relates to the fact that participants were already familiarized with the stimulus set prior to the experiment. Therefore, the observed view-independence may only apply to previously seen faces but not to strictly novel unfamiliar faces. In order to avoid this possible confound of pre-experimentally acquired familiarity, Experiment 2 used a new set of completely novel faces.

Initially novel unfamiliar faces rapidly become familiar after a few encounters, which might result in qualitative changes in the underlying face recognition processes. Experiment 2 (see Chapter 4) tested this hypothesis by comparing N250r components to repeated presentations of unfamiliar faces when these were still ‘strictly unfamiliar’ (in the first half of the experiment) as compared to ‘visually familiar’ (in the second half). Faces were presented in two views: a front view or side view (rotated by 45°). Two images on each trial showed either the same, or two different individuals in either the same or two different views. Overall analyses showed that N250r amplitudes were unaffected by view repetitions versus changes, and therefore view-invariant. It has to be noted that an interaction between identity and view nearly reached significance indicating a lack of statistical power. Therefore, larger N250r responses to repetitions of the same face in the same as compared to a different view suggests that unfamiliar face recognition is not strictly view-invariant but also shows a degree of view-specificity.

When separate analyses were run for first and second experimental half, it became apparent that view-independent face recognition only emerged in the second half of the experiment as a result of face learning. During the first experimental half, an N250r was only

present on view-repetition trials, but was absent on view-change trials, suggesting that identity-matching processing were initially based on low-level *pictorial* information. In contrast, an N250r component was present on both view-repetition and view-change trials in the second half of the experiment after facial identities had been learned. These findings provide electrophysiological evidence, which demonstrates, for the first time that experimentally acquired visual familiarity with initially novel faces results in qualitative changes in the way in which these faces are processed and represented in memory. These changes could either reflect the acquisition of *structural* codes for facial identity (see Bruce & Young, 1986) or the formation of associative links between sets of distinct view-specific images of the same person (see Longmore et al., 2008).

The roles of attention and WM in face identity processing

In order to recognize a familiar face, incoming perceptual information must be matched against representations of faces stored in memory. This requires the formation of a visual face memory trace, and its maintenance over a period of time. One interesting question concerns the role of attention and/or strategic processing for face identity processing. Are identity-specific cues of unfamiliar faces processed in an optional or obligatory fashion? Considering the ease with which human faces are distinguished in daily life, it appears plausible to assume that individual face recognition reflects a degree of mandatory processing, irrespective of a person's intentions. In particular, research suggests that information about identity is processed in an automatic manner, when faces are familiar (e.g., Buttle & Raymond, 2003; Ellis et al., 1990). Therefore, the activation of long-term memory representations of familiar faces may be unstoppable, while attention may or may not be needed to extract identity-related facial cues from unfamiliar faces.

To explore the mechanisms of attention on unfamiliar face recognition, Experiments 3-5 studied whether N250r components would be observed during identity-unrelated *implicit* tasks. In Experiment 3 (see Chapter 5), a clear N250r component emerged to repeated presentations of the same individual face in a view-matching task where participants performed same/different view judgments and facial identity was task-irrelevant. This finding suggests that information about the identity of unfamiliar faces is processed in a mandatory fashion during identity-unrelated tasks that require the maintenance of a particular facial feature in visual memory. To further assess the task-dependence of individual face

recognition processes, Experiments 4 and 5 (see Chapter 6) measured N250r components during two tasks: face identity matching (*explicit*), and target detection (*implicit*) where responses were required to infrequent inverted faces. Experiment 4 used images of unfamiliar faces, where an N250r was elicited for the *explicit* task, but was absent for the *implicit* task, suggesting a strong task-dependence of the underlying face recognition mechanisms. Moreover, the observation that perceptual face representations were not maintained in WM when participations made immediate responses to inverted face targets in the *implicit* task suggests that identity-specific facial cues are not automatically encoded in tasks that do not have a memory component. Although facial identity was task-irrelevant in both Experiments 3 and 4, the critical difference was that information about the first face had to be maintained in WM in order to perform the view-matching task in Experiment 3. In contrast, the task of detecting infrequent inverted face targets in Experiment 4 had no such memory component. However, this observed task dependence of face identity processing might be related to the fact that face stimuli were unfamiliar in Experiment 4. This hypothesis was tested in Experiment 5 where images of famous celebrities were repeatedly presented during *explicit* and *implicit* tasks (i.e., detection of inverted face targets). N250r responses were clearly elicited for the *explicit* task but not for the *implicit* task for both unfamiliar and famous faces, demonstrating that early perceptual face recognition processes are unaffected by visual familiarity.

In face matching tasks, perceptual face representations need to be actively maintained in visual memory so that they can be re-activated when the same individual face is repeated. How stable are these WM representations over longer time intervals between face repetitions? Experiment 6 (see Chapter 7) addressed this question by comparing N250r amplitudes during short and long interstimulus intervals (ISIs of 200 ms versus 1200 ms) while participants performed a view-matching task. The reliable presence of an N250r across ISIs demonstrated the robustness of visual-short term memory for unfamiliar faces over short periods of time. However, results showed that the strength of perceptual face memories decreased when these had to be maintained over long ISIs, which is likely to reflect the decay of visual face memories over time. This memory-related decay was observed for both trials where two faces were repeated in either the same view, or a different view, indicating similar mechanisms of decay for both *structural* and *pictorial* representations.

Face identity processing in DP

Important insights into the complex architecture of human face perception can be obtained by studying cases where face recognition fails, as for example in developmental prosopagnosia (DP). While Experiments 1-6 addressed the neural mechanisms of face processing in adults with typical face recognition abilities, Experiment 7 (see Chapter 8) tested the presence and nature of neural markers of unfamiliar face recognition in a group of ten DPs in an *implicit* view-matching task that required same/different view judgments on pairs of unfamiliar faces. On each trial, two faces either showed the same, or two different faces, in either the same, or two different views. The main research question was whether DPs process identity-related information about unfamiliar faces in a task context where facial identity is irrelevant. In addition, it was tested whether DPs are particularly impaired in processing abstract view-invariant information about facial identity, which is required on trials with a view change.

Results showed that a reliable N250r was elicited by same face repetitions in both control and DP groups. Most importantly, N250r components showed very similar amplitudes and scalp topographies across both groups, indicating a degree of spared normality of early perceptual face recognition processes in the tested DPs. However, N250r amplitudes in the DP (but not control participants) tended to be smaller when view changed between repetitions relative to identical-view repetitions, presumably reflecting inefficient processing of invariant face structure in DP. In addition, there was also evidence for implicit learning of the identity of unfamiliar faces in the DP group when initially novel unfamiliar faces had become more familiar. Overall, the findings support the view that face recognition deficits in developmental prosopagnosia result from localized impairments, which can selectively occur at late post-perceptual processing stages while early perceptual face mechanisms are largely intact. This suggests that face recognition deficits in DP do always result from impaired visual face memory, but can reflect an inability to access semantic face memory. The proposed dissociation between intact perceptual and impaired post-perceptual face recognition processes not only suggests that early and late face processing stages operate to some extent independently, but also emphasizes the importance of later processing stages for conscious face recognition.

Experiment 7 had several limitations including the small sample size of the DP group and a resulting lack of statistical power. In addition, control and DP groups were not age-matched

and the fact that DP participants were on average 12 years older than control participants leaves open the possibility that atypical ERP responses in the DP group reflect changes related to ageing rather than prosopagnosia. In addition, neural changes associated with face learning could not be examined in participants with normal face recognition abilities, as these were already familiar with the face stimulus set. Therefore, a follow-up study is needed to fully interpret the present findings.

9.2 Future directions

The findings of the present thesis give rise to several directions for future research on human face perception. One possible avenue would be to conduct a combined EEG-fMRI study, allowing excellent temporal and spatial resolutions, and the localization of the neural sources of N250/N250r components, which have been linked to the fusiform gyrus. A different approach would be to measure ERPs during a typical behavioural face learning study, where the time interval between learning and recognition is usually much longer than in event-related face paradigms. Such a design would provide insights into the basis of the discrepancies between ERP and behavioural measures regarding the image-dependence or independence of face recognition processes, with the former demonstrating largely view-dependent and the latter a degree of view-independent face recognition. Studying N250r markers of face identity processing over longer time intervals between learning and recognition would not only more closely mirror everyday demands on face recognition memory, but also provide new insights into the persistence of view-independent unfamiliar face recognition over time. Thus, while the research presented in this thesis has focused on visual short-term memory, future studies could investigate the mechanisms that underlie long-term face memory, and in particular the mechanisms that are involved in face learning over longer periods of time (e.g., several hours or days).

Another interesting direction for future research would be to further clarify the mechanisms of perceptual face learning. For example, is face learning facilitated when visual and semantic facial cues are simultaneously encoded? Which factors boost the perceptual representation of faces in memory (e.g., facial distinctiveness or encoding strategy)? Insights into how the human brain most effectively encodes and stores new face representations are important to develop training programs for adults or children with face recognition impairments. In particular, the observation of intact perceptual face processes in some

individuals with DP implies that visual training is likely to be ineffective in these cases, as severe face recognition impairments do not appear to result from early perceptual deficits in face processing. Instead, strengthening the links between semantic and visual cues during face learning might aid face recognition memory in those individuals. A related question about face learning concerns the number of encounters that are required to allow the transition from temporary to more permanent storage of visual face memories. Thus, the role of various factors in aiding individual face recognition needs to be further investigated.

Overall, while the present thesis adds to our understanding of the neural processes that mediate the perception and recognition of individual faces, many questions about the complex neural architecture of the human face processing system are still not fully understood. In this context, the importance of faces for cognitive and neuroscientific research extends beyond the modular/expertise debate, and includes more general insights into the brain mechanisms and processes of highly skilled visual systems that have developed for socially important stimuli.

9.3 Summary and implications

Understanding how the human brain perceives and remembers individual faces has become one of the most exciting areas of research in face perception (e.g., Kanwisher, 2000; Haxby et al., 2000). New insights in recent years have led to many important advances in our understanding of the complex nature of human face processing. However, several important questions about the mechanisms that underlie our ability to perceive and recognize unfamiliar faces are still unresolved. The present thesis has provided novel insights into the neural processes that mediate early perceptual stages of unfamiliar face recognition and face learning. The ERP data presented here have not only provided evidence for view-independent face recognition but also demonstrate, for the first time, a qualitative shift from view-dependent to view-independent recognition during face learning (Experiments 1 and 2). Furthermore, although face recognition processes show a degree of mandatory processing of identity-specific cues, face identity processing is not a fully automatic phenomenon, but a dynamic process that is modulated by cognitive factors such as task relevance and attention (Experiments 3 and 4). However, task-dependent modulations of early stages of visual face recognition appear to be independent of the previous familiarity of faces (Experiment 5). While perceptual face memories show a degree of robustness across pictorial changes (i.e.,

view), the strength of face memory traces decreases when they need to be maintained in WM over longer periods of time (Experiment 6). Finally, severe face recognition deficits in individuals with developmental prosopagnosia (DP) are, in some cases, not linked to impaired perceptual face recognition processes, indicating a dissociation between spared visual and impaired semantic face memory (Experiment 7).

The current findings provide evidence for a high-level abstract representation of facial identity, which closely relates to the concept of face recognition units (or FRUs) in Bruce and Young's (1986) functional model where each FRU contains stored descriptions of the unique facial features of an encountered face. The emergence of the N250r ERP response during face learning therefore suggests that FRUs are acquired in a fast and effortless manner following repeated exposure with the same novel face across different viewing conditions. Linking event-related brain responses to Bruce & Young's functional sub-components for face recognition further highlights the fast stream of face processing where successful recognition of a previously encountered face occurs within 300 ms. Furthermore, the observed top-down task dependence of identity processing demonstrates the important role of selective attention for successful face recognition. Finally, the observation of spared perceptual face recognition processes in DP confirms the serial and distributed nature of human face perception where visual and non-visual facial information is processed by functionally independent brain regions (see Haxby et al., 2000).

Taken together, the present insights add to our current knowledge of human face perception by demonstrating that unfamiliar face recognition involves the acquisition of abstract visual face memories that emerge during face learning, and reflect fast and flexible (i.e., strongly task-dependent) neural processes for the perception of facial identity.

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